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The Reproductive Ecology of Two Sympatric Demersal Fishes: The Naked Goby Gobiosoma bosc and Striped Blenny Chasmodes bosquianus

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THE REPRODUCTIVE ECOLOGY OF TWO SYMPATRIC DEMERSAL FISHES: THE NAKED GOBY *GOBIOSOMA BOSC* AND STRIPED BLENNY *CHASMODES BOSQUIANUS*

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ABSTRACT

The naked goby (*Gobiosoma bosc*) and striped blenny (*Chasmodes bosquianus*) are sympatric oyster reef fishes within temperate estuaries. The reproductive biology and early life history of these fishes were described during two consecutive spawning seasons from 2012-2013 in North Inlet, SC. The naked goby and striped blenny spawning seasons lasted for 21 weeks and 30 weeks, respectively, for 2012 and 2013. The naked goby spawning season began 3 weeks later than the striped blenny spawning season for both years. The temporal offset in the start of their spawning seasons may reduce competition for nest habitat between the two species. Naked gobies produced more oocytes female^{-1} (1,024- 2,616) than striped blennies (148- 585) despite their generally smaller length (29-36 mm SL, goby; 44-56 mm SL, blenny). However, striped blenny larvae were larger than naked goby larvae at hatch (2.76-3.60 mm TL, goby; 2.93-4.32 mm TL, blenny). Growth rates increased by 0.07 mm day^{-1} for naked gobies and 0.05 mm day^{-1} for striped blennies after week 10 of their spawning seasons when water temperature was >28°C. Increased growth rates allowed late-season larvae to reach flexion and settlement faster than early-season larvae. Faster naked goby growth rates allowed late season larvae to reach settlement lengths similar to those observed for early season larvae (6.42-9.0 mm TL) in 20-21 days versus 19-30 days for early season larvae. Striped blenny average settlement length decreased from 9.32±0.28 mm TL by 26% between weeks 6 and 18 of the spawning season. Striped blenny larval duration ranged from 14-23 days. The differences observed in the early life history and reproductive biology of naked gobies and striped blennies allow for temporal habitat partitioning during the adult and larval phases and reduce competition between the two species.

INTRODUCTION

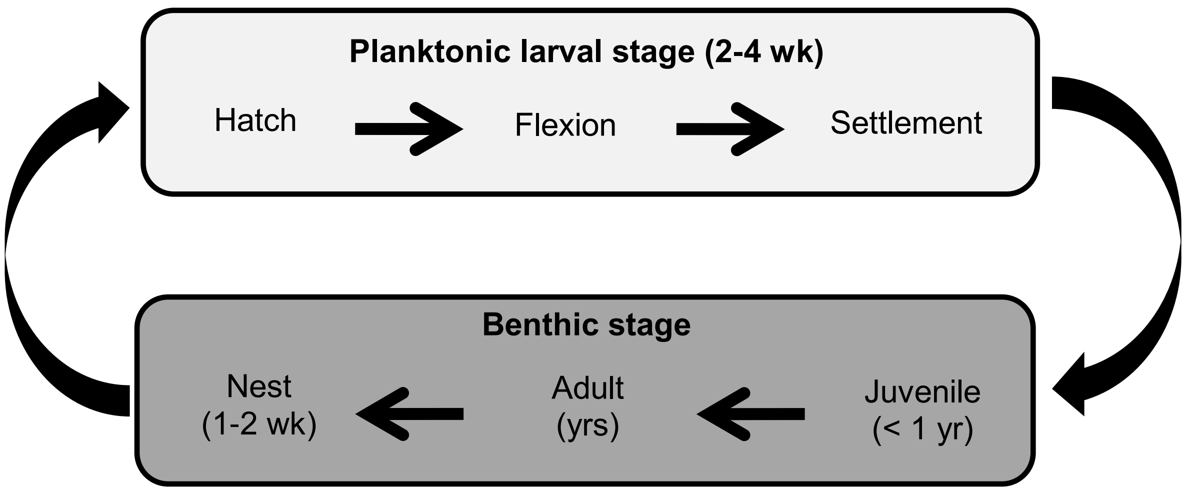
Estuaries are highly productive and variable ecosystems that support diverse communities (Boesch and Turner 1984; Zimmerman et al. 1989; Coen et al. 1999; Stunz et al. 2010). Most temperate estuaries along the South Atlantic Bight (North Carolina, South Carolina, Georgia, and northeastern Florida) contain reefs formed by the Eastern oyster *Crassostrea virginica* (Wells 1961; Bahr and Lanier 1981; Dame et al. 2000). Oyster reefs are common to bar-built and lagoon-marsh estuaries and may be intertidal or subtidal, patch or fringing (i.e., lining the shores of tidal creeks), and range in size from small scattered oyster clumps to large three-dimensional structures of living and dead shell (Bahr and Lanier 1981; Coen and Luckenbach 2000; Dame et al. 2000).

Living oyster reefs play a role in nutrient recycling and benthic pelagic coupling within the estuarine system (Newell 1988; Dame et al. 1989; Gerritsen et al. 1994; Coen and Luckenbach 2000; Dame et al. 2000; Newell 2004; Newell et al. 2005). Oyster populations may help control phytoplankton standing stocks and reduce the susceptibility of estuaries to eutrophication because they are filter feeders (Officer 1982; Newell 1988, 2004; Dame et al. 2000). Oysters also play a role in the removal of particulate inorganic matter (PIM) and particulate organic matter (POM) from the water column (Dame et al. 1989; Gerritsen et al. 1994; Newell et al. 2005). Undigested PIM and POM that has been filtered by oysters is excreted as mucus-bound pseudofeces, increasing water clarity (Newell 1988, 2004; Dame et al. 1989; Gerritsen et al. 1994). Oyster populations remineralize particulate nitrogen (phytoplankton) to ammonium, a preferred nutrient for plants, thus completing a feed-back loop between marsh-estuarine and coastal ocean systems (Dame et al. 1986, 1989; Newell 2004).

Oyster reefs provide structurally complex habitat within systems that are otherwise dominated by unvegetated soft-bottom areas (Bahr and Lanier 1981; Gutiérezze et al. 2003; Grabowski and Powers 2004). Like coral reefs, oyster reefs form living three-dimensional structures that provide food, habitat, and settlement substrate for many fish and invertebrate species (e.g., Wells 1961; Bartol and Mann 1997; Coen and Luckenbach 2000). Biogenic habitats like oyster reefs create various microhabitats as a result of their heterogenetic structures (Wells 1961, Bartol and Mann 1997, Tolley and Volety 2005, Humphries et al. 2011). As a result, subtidal and intertidal oyster reefs have higher species density and greater species diversity compared to adjacent soft-bottom areas (Harding and Mann 1999, Coen and Luckenbach 2000, Stunz et al. 2010, Humphries et al. 2011). Therefore, living oyster reefs are temperate analogs to tropical coral reefs (Grabowski and Powers 2004).

Many tropical and temperate reef fishes exhibit a bi-phasic life cycle that consists of a benthic adult stage and a planktonic larval stage (Sale 1980; Doherty 1991; Leis 1991; 2010; Victor 1991; Figure 1). Advantages associated with a planktonic larval phase include dispersal into new habitats, avoidance of competition for resources with benthic adults, and the reduction of benthic-associated mortality (Leis 1991). Most adult reef fishes are sedentary (Sale 1980, 1982; Leis 1991), and larvae may disperse to broader ranges than their adult counterparts through tides and currents (Fortier and Leggett 1982, 1984; Leis 1986). Therefore, the planktonic larval stage influences adult population size and geographic range (Doherty 1983; Leis 1991). Successful recruitment to a reef and survival after settlement may be influenced by larval growth (Houde 1987, 1989; Pepin 1991).

Figure 1: The bi-phasic life cycle of naked gobies and striped blennies from planktonic larvae into benthic adults.


Planktonic larval stage (2-4 wk)
Hatch
Flexion
Settlement
Benthic stage
Nest
(1-2 wk)
Adult
(yrs)
Juvenile
(< 1 yr)

The likelihood that early life history dynamics will be affected by food availability, predation, or environmental factors like water temperature is driven by the timing of adult spawning (Houde 1997). Therefore, annual spawning cycles are synchronized with environmental factors (e.g., water temperature, day-length, lunar cycles) that result in fish larvae being present during optimum environmental and food conditions. Changes in annual water temperatures may influence spring and summer spawning fishes to spawn earlier in the year if their spawning cycles are synchronized with increasing water temperatures (Shoji et al. 2011; Zucchetta et al. 2012; Laur et al. 2014). Changes in the timing of plankton blooms or fish spawning could offset the interaction between first-feeding larvae and their prey (Hjort 1914; May 1974; Cushing 1990).

The time to maturation and the amount of energy that is allocated into reproduction are aspects associated with fish reproductive strategies (Hutchings 1997). Fish reproductive strategies fall along an r-K- continuum where different environmental and biological pressures may select for individuals that mature early and produce many smaller offspring (r-selected species) or select for individuals that mature later and produce fewer larger larvae (K-selected species; MacArthur and Wilson 1967; Pianka 1970). Energy available after the cost of maintenance metabolism is typically allocated to growth or reproduction (Warren and Davis 1967; Franco et al. 2003). Energy allocated to reproduction may be divided between behavioral components such as nest-building or physiological components like the number of eggs deposited by a female (Hutchings 1997).

The reproductive strategies exhibited by fishes are influenced by density-independent and density-dependent processes that affect larvae and juveniles (Houde 1987; Smith 1978). Planktonic larvae are subject to density-independent events such as changes in water temperature, while newly settled larvae are subject to density-dependent processes including competition for food and habitat (Victor 1983, 1986; Smith and Tyler 1972; Smith 1978). Species composition and diversity within a reef community may be due to stochastic events or result from niche partitioning and competition (Smith 1978). Some reproductive strategies may be more advantageous than others depending on the factors that influence larval and juvenile processes within an ecosystem (Jones 1991). Variable or harsh physical factors that result in high mortality favor species which mature early and produce many offspring (Dobzhansky 1950). Conversely, in areas where environmental factors are stable, biological interactions favor species that are better able to compete for resources (Dobzhansky 1950).

The naked goby *Gobiosoma bosc* (Lacépède 1800) and striped blenny *Chasmodes bosquianus* (Lacépède 1800) are sympatric (i.e., inhabit the same geographic area; Hardin 1960) demersal fishes present in temperate U.S. Atlantic estuaries (Fritzsche 1978; Able and Fahay 1998). Naked gobies and striped blennies are two members of a guild of demersal oyster reef fishes that exhibit similar reproductive strategies and occupy the same trophic level in temperate estuaries (e.g., darter goby, *Ctenogobius bolesoma;* seaboard goby, *Gobiosoma ginsburgi;* highfin goby, *Gobionellus oceanicus;* clown goby, *Microgobius culosus;* green goby, *M. thalassinus;* crested blenny, *Hypleurochilus geminatus;* feather blenny, *Hypsoblennius hentz;* freckled blenny, *H. ionthas,* Zingmark 1978). These fishes may live in oyster reef habitats and use oyster reefs for foraging and nesting sites (Hildebrand and Cable 1938; Dawson 1966; Dahlberg and Conyers 1973; Nero 1976; Crabtree and Middaugh 1982). These fishes feed on infaunal and epibenthic invertebrates (Hildebrand and Schroeder 1928; Dahlberg and Conyers 1973) present on the oyster reef. They may be eaten by larger piscivorous fishes including red drum *Scianops ocellatus*, black drum *Pogonia cromis*, Atlantic croaker *Micropogonias undulatus*, and summer flounder *Paralichthys dentatus* (Dawson 1966; Nero 1976). Thus, gobies and blennies provide connectivity between trophic levels within estuarine food webs.

Gobies and blennies exhibit reproductive strategies in which females deposit sequential clutches throughout a spawning season into nests that are guarded by a male (Hildebrand and Cable 1938; Nero 1976; Ditty et al. 2005). Males fertilize the oocytes after deposition and then tend the developing embryos for 1-2 weeks until hatch (Hildebrand and Cable 1938; Nero 1976). Nests are typically laid within empty articulated oyster shells (Hildbebrand and Cable 1938; Nero 1976; Crabtree and Middaugh 1982). After hatch, larvae remain planktonic for 2-4 weeks until settlement (Hildebrand and Cable 1938; Breitburg 1989; Harding and Mann 2000).

In North Inlet, South Carolina, the naked goby and striped blenny occur with other sympatric species that occupy local oyster reefs (Crabtree and Middaugh 1982; Lehnert and Allen 2002). These species may partition habitat both spatially and temporally to allow their coexistence on oyster reefs. The naked goby and striped blenny deposit nests more frequently at shallow depths (< 0.30 m below mean low water) compared to the other Gobiidae and Blenniidae species in North Inlet (Crabtree and Middaugh 1982). Therefore, these two species are more likely to compete for food and habitat resources in North Inlet tidal creeks. This thesis will describe the reproductive and larval biology of the naked goby and striped blenny. Differences in naked goby and striped blenny life reproductive ecology may reduce niche overlap and competition between the two species.

Temporal offsets in the timing and duration of the naked goby spawning season may constrain available nest sites for each species. The proportion of energy allocated into gonad development will influence early life history dynamics and subsequently recruitment success (Hutchings 1997). The timing and duration of annual reproductive cycles and the reproductive biology of the naked goby and striped blenny are described and related to community- and ecosystem-level processes that influence their reproductive cycles in Chapter 1: The reproductive biology of two sympatric demersal fishes, the naked goby (*Gobiosoma bosc*) and striped blenny (*Chasmodes bosquianus*).

Adults that invest energy into fewer larger larvae may produce offspring that have an advantage over larvae that are smaller (Hunter 1981). Larger larvae are better able to swim, making them less vulnerable to predation and more successful at capturing prey (Hunter 1981; Bailey 1984; Bailey and Batty 1984). However, larvae that are smaller but are produced at a greater abundance may sustain lower cohort mortality due to density-independent factors during their larval phase (Houde 1987, 1989). Furthermore, the plasticity observed in larval fish early life history may differ between species and during the spawning season as water temperature increases. Faster growth rates may result in shorter larval periods which reduce exposure to planktonic risks. Naked goby and striped blenny early life history and the variability of hatch length, larval period duration, settlement length, and growth rate during the spawning season were described in Chapter

2: Early life history of the naked goby (*Gobiosoma bosc*) and striped blenny (*Chasmodes bosquianus*).

These two chapters provide data that are used to qualitatively and quantitatively describe the reproductive ecology of two sympatric species present in southeastern temperate estuaries. These data are used to assess the ecosystem-level processes that have influenced species-specific life histories and how these processes allow for the co-existence of several sympatric species within the same oyster reef habitat. Furthermore, these data document the natural variability observed in naked goby and striped blenny early life history over the spawning season in relation to ambient increases in water temperature.

CHAPTER 1:
REPRODUCTIVE BIOLOGY OF THE NAKED GOBY (*GOBIOSOMA BOSC*) AND STRIPED BLENNY (*CHASMODES BOSQUIANUS*)

ABSTRACT

The naked goby (*Gobiosoma bosc*) and striped blenny (*Chasmodes bosquianus*) are sympatric demersal fishes present in temperate estuaries. Environmental cues (e.g., temperature, day-length) drive temperate fish reproductive cycles. Spawning season duration was estimated by monitoring fish nesting activity on oyster reefs. Gonadosomatic indices (GSI) were used to describe annual reproductive cycles in North Inlet, SC during 2012 and 2013. Clutch size (oocytes female^{-1}) and oocyte diameter were measured. The naked goby and striped blenny spawning seasons lasted for 21 weeks and 30 weeks, respectively, for both years. GSI values ranged between 0-8% (goby and blenny males), 0-28% (goby females), and 0-6% (blenny females). Female goby and blenny GSI values increased with increasing day-length. Female blenny GSI values were also correlated with increasing water temperature, but male blenny GSI values decreased with increasing water temperature. Decreases in male GSI values are likely due to parental care exhibited during nest development. Clutch size ranged between 1,024 and 2,616 oocytes female^{-1} for naked gobies 29-36 mm standard length (SL), and between 148 and 585 oocytes female^{-1} for striped blennies 44-56 mm SL. Goby oocyte diameters (0.42-0.78 mm, n = 360) were approximately half the size of blenny oocyte diameters (0.75-1.16 mm, n = 360). The differences in clutch size and reproductive investment exhibited by these two sympatric fishes represent different reproductive strategies along the r-K-continuum that are adapted to their species-specific life history.

INTRODUCTION

Temperate marine fish reproductive cycles are driven by species-specific endogenous rhythms that are synchronized with environmental cues (Qasim 1955; Bye 1984; Stacey 1984; Dembsky et al. 2006). Endogenous factors (e.g., hormones, steroids) control gonad development and maturation (Stacey 1984). The initiation of spawning is synchronized with responses to environmental (e.g., water temperature, day-length, lunar phase), physiological (e.g., hormonal), and behavioral (e.g., nest-building) cues (Bye 1984). Water temperature and day-length are the two most important environmental cues that affect temperate fish reproductive cycles (Bye 1984; Stacey 1984; Dembsky et al. 2006).

Fish gonad development occurs when water temperatures exceed a minimal threshold of 10°C for most temperate fishes (Bye 1984; Stacey 1984). Gonad development may be asynchronous (oocytes of all developmental stages are present) or synchronous (all oocytes develop and ovulate at the same time; Balon 1984; Murua et al. 2003). Asynchronous gonad development typically occurs within species that spawn multiple times within a single reproductive season, whereas synchronous gonad development typically occurs within species that only spawn once per year (Murua et al. 2003). Spawning, which includes the acts of courting and mating, may occur once (semelparity) or may be repeated (iteroparity) throughout the lifespan of a fish (Balon 1984).

A gonadosomatic index (GSI), a comparison of the percentage of gonadal to total tissue weight, describes fish reproductive investment while removing variability attributed to size (Miller 1984; Wilk et al. 1990). Energy available after the cost of maintenance metabolism is typically allocated to growth or reproduction (Warren and Davis 1967; Franco et al. 2003). Energy allocated into reproduction may be partitioned among many smaller offspring (r-selected species) or fewer larger offspring (K-selected species; MacArthur and Wilson 1967; Pianka 1970). Increases in gonadosomatic index values represent increases in gonadal (or reproductive) investment, and indicate spawning (Way et al. 1998).

Most physiological variables (e.g., gonad weight; fecundity) vary non-linearly (i.e., allometrically) with increasing body weight (Smith 1984; Packard and Boardman 1987). The proportion of heat loss (a function of surface area) to heat production (a function of body mass) increases with decreasing body size (Livingston 2001). Smaller animals expend more energy maintaining heat loss, which increases their cost of metabolism and decreases their scope for growth (i.e., the energy available for somatic and reproductive growth; Livingston 2001). Conversely, relationships that scale linearly are isometric relationships. In such cases, a doubling of body size equals a doubling in the other variable (e.g., body depth; Packard and Boardman 1987).

Spawning onset and duration for temperate marine fishes may be adapted to provide optimal food and environmental conditions for larvae and adults (Qasim 1955; Bye 1984; Miller 1984; Cushing 1990). In temperate and subtropical regions, sufficient food availability for both the adults and larvae allows for extended (> 5 months) spawning seasons (Qasim 1955; Johannes 1978). Species that produce larvae during extended spawning seasons ensure that their larvae co-occur with optimum food and environmental conditions (Qasim 1955; Johannes 1978; Lambert and Ware 1984).

Estuarine fishes have evolved reproductive strategies that are adapted for life in ephemeral habitats (Dando 1984). Estuarine temperature, salinity, oxygen concentration, and turbidity may fluctuate temporally and spatially (Dando 1984). Species may migrate from estuaries to spawn in coastal marine waters, where salinity and temperature are more stable (e.g., sand goby, *Pomatoschistus minutus,* Gobiidae; summer flounder, *Paralichthyes dentatus,* Paralichthyidae; Pearcy and Richards 1962; Dando 1984). Some fishes that spawn within the estuary (e.g. naked goby, *Gobiosoma bosc*, Gobiidae; striped blenny, *Chasmodes bosquianus*, Blenniidae) have demersal eggs to reduce the chances of egg transport out of the estuary (Hildebrand and Schroeder 1928; Hildebrand and Cable 1938). Naked goby and striped blenny females may deposit multiple sequential batches of eggs (or clutches) into nests during the spawning season and nests may contain eggs from multiple females (Hildebrand and Cable 1938; Nero 1976). Many species that deposit demersal eggs have developed parental care behaviors (e.g., *G. bosc, C. bosquianus*) to reduce egg predation and mortality due to siltation (Hildebrand and Cable 1938; Potts 1984). Naked goby and striped blenny males defend, clean, and fan the nest from deposition until hatch (Hildebrand and Cable 1938; Dawson 1966; Dahlberg and Conyers 1973; Nero 1976; Crabtree and Middaugh 1982). After hatch, naked goby and striped blenny larvae remain planktonic for 2-4 weeks, depending on water temperature, until they settle onto the benthos and metamorphose into juveniles (Hildebrand and Cable 1938; Breitburg 1989; Harding and Mann 2000).

Naked gobies and striped blennies use oyster habitats for foraging and nesting sites (Hildebrand and Cable 1938; Dawson 1966; Dahlberg and Conyers 1973; Nero 1976; Crabtree and Middaugh 1982). These fishes are generalists that feed on infaunal and epibenthic invertebrates (Hildebrand and Schroeder 1928; Dahlberg and Conyers 1973). Naked gobies and striped blennies use articulated oyster valves for nesting sites and refuge (Hildebrand and Cable 1938; Dahlberg and Conyers 1973; Crabtree and Middaugh 1982). Nesting sites are selected depending on the shell gape size relative to adult fish length (Dahlberg and Conyers 1973, Crabtree and Middaugh 1982).

The beginning of the naked goby and striped blenny spawning season coincides with increasing water temperatures (>16°C) and day-length (>12 hr) during spring (Mar-May; Table 1). Spawning continues through the summer (June-August) and terminates in fall (September-November) for both species (Dawson 1966; Dahlberg and Conyers 1973). Spawning season duration increases with decreasing latitude (Table 1). Naked goby and striped blenny spawning may occur for 4-5 months in northern estuaries and as long as 6-7 months in southern estuaries (Table 1).

The annual reproductive cycles of naked gobies and striped blennies were described in North Inlet, SC during 2012 and 2013. GSI values were calculated and described in relation to water temperature (°C) and day-length (hr) for both naked gobies and striped blennies. Naked goby and striped blenny spawning season duration was estimated by monitoring nesting activity on North Inlet oyster reefs. Clutch size (oocytes female^{-1}) and oocyte diameter (mm) were estimated for fishes collected between April and August to describe female gonad development.

Table 1: Summary of naked goby and striped blenny life history metrics reported within their geographic range. Data that were not applicable are indicated by NA. Day-length data for each location were retrieved from the U.S. Naval Observatory (usno.navy.mil).

Species	Location	Spawning season (mo.)	Water temp. (°C)	Day-length (hr)	SL range male (mm)	SL range female (mm)	No. oocytes female^{-1}	Egg diameter (mm)	Nest development (d)	Hatch length (mm)	Settlement length (mm)
Naked goby	Long Island, NY[1]	May-August	16-21	14.0-15.1	NA	NA	NA	NA	NA	NA	NA
	Breakwater harbor, DE[1]	May-September	17-20	13.8-14.8	NA	NA	NA	NA	NA	NA	NA
	Patuxent River, MD[2]	May-August	17-25	13.8-14.8	NA	NA	NA	NA	NA	3.00	10.0
	York River, VA[3]	May-August	18-27	13.7-14.7	NA	NA	NA	NA	NA	<4.00	10.0-14.0
	Chesapeake Bay, VA[4]	May-September	15-30	13.7-14.7	25-60	NA	NA	NA	NA	2.00	10
	Lynnhaven, VA[5]	April-August	18-29	13.6-14.7	14-46	14-35	622-1418	0.05-0.62	5-9	2.48	10.6
	Beaufort, NC[6]	May-September	16-28	13.5-14.4	NA	23-30	249	0.52-0.59	5	2.00	10.0
	North Inlet, SC[7]	April-September	20-30	12.5-14.4	32-52	NA	NA	NA	NA	NA	NA
	Sapelo Island, GA[1]	April-August	20-30	12.5-14.2	18-51	27-35	701-1382	0.17-0.60	NA	NA	NA
	Mississippi Sound, MS[8]	April-October	20-30	12.5-14.1	7.3-36.4	NA	NA	NA	NA	NA	7.30-12.0
	Alazan Bay, TX[9]	April-November	20-30	12.5-13.9	NA	NA	NA	NA	NA	NA	NA
Striped blenny	Chesapeake Bay, VA[4]	April-August	15-30	12.6-14.7	25-90	NA	NA	NA	NA	NA	NA
	Beaufort, NC[6]	May-August	16-28	13.5-14.4	<60	<60	NA	0.93-1.10	11	3.56-3.78	10.0-12.0
	North Inlet, SC[7]	April-September	20-30	12.5-14.4	49-79	NA	NA	NA	NA	NA	NA

[1]Dahlberg and Conyers (1973)
[2]Shenker et al. (1963)
[3]Massmann et al. (1963)
[4]Hildebrand and Schroeder (1928)
[5]Nero (1976)
[6]Hildebrand and Cable (1938)
[7]Crabtree and Middaugh (1982)
[8]Dawson (1966)
[9]Dokken et al. (1984)

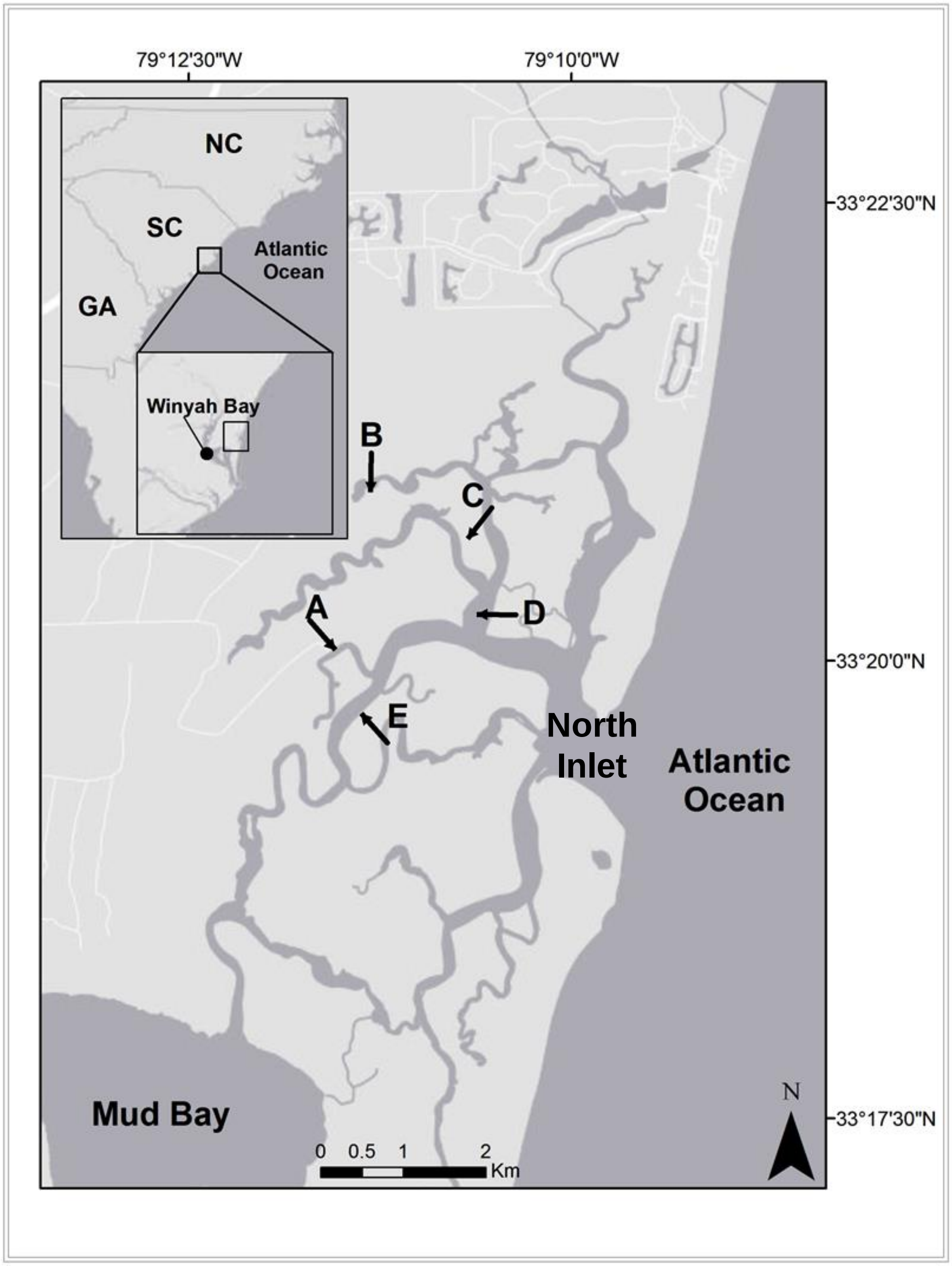
METHODS

Environmental data. North Inlet, South Carolina is a tidally dominated, high salinity estuary (Novakowski et al. 2004). Three main channels branch into dozens of sub-tidal creeks, and over 1,000 intertidal creeks (Novakowski et al. 2004). *Spartina alterniflora* salt marsh (73%) dominates the majority of North Inlet habitat area. Tidal creeks, mud flats, and fringing *Crassostrea virginica* oyster reefs comprise 20.6%, 5.4% and 1% of North Inlet habitat area, respectively (Dame et al. 1986). North Inlet experiences an annual semidiurnal tidal range of 1- 2.5 m (Kjerfve et al. 1981) and a typical tidal depth of 3-5 m (Chrzanowski et al. 1982; Dame et al. 1986; Novakowski et al. 2004).

An automated monitoring station in Crabhaul Creek, North Inlet records water temperature (°C) and salinity every 15 minutes (NERR CDMO; cdmo.baruch.sc.edu). Average weekly water temperatures and salinities (672 readings per week) from Crabhaul Creek were used to describe ambient conditions from January 1, 2012, through December 31, 2013. Cumulative week of the years (CumWOY) was used to describe sampling week during the two year period from the week of January 1, 2012 (CumWOY 1) through the week of December 29, 2013 (CumWOY 104). Day-length (hr) data were obtained for Georgetown, South Carolina, from the U.S. Naval Observatory (usno.navy.mil).

Spawning season duration and nest observations. Observations of naked goby and striped blenny nest presence/absence were made approximately every week from May through November 2012 and from March through November 2013 on fringing oyster reefs (Figure 2) to estimate spawning season duration. Observations were conducted for ~3 hr on each date. The number of naked goby and striped blenny nests observed in oyster shells was recorded. The beginning and end of the fish spawning seasons were

Figure 2: Tidal creeks in North Inlet, SC (33°N; 79°W) where nest observations and fish collections occurred including Clambank (A), Crabhaul (B), Bly (C), Old Man (D), and Town Creeks (E).


79°12'30"W
79°10'0"W
33°22'30"N
33°20'0"N
33°17'30"N
NC
SC
GA
Atlantic Ocean
Winyah Bay
A
B
C
D
E
North Inlet
Atlantic Ocean
Mud Bay
N
0 0.5 1 2
Km

estimated using the mean day of the year (DOY) between the first or last observed nest DOY and the next closest sampling date. For example, if naked goby nests were first observed on April 18, 2013 (DOY 108) and the last observation made before that date was April 10, 2013 (DOY 100), then the onset of the spawning season was calculated using the equation:

$$\text{Onset}=\frac{108+100}{2}=104$$

Likewise, the end of the spawning season was estimated using the mean DOY between the last observed nest and the next date of observations.

Adult fish collection. Adult naked gobies and striped blennies were collected every four weeks from June 2012 through November 2013. Fish were collected at low tide on fringing intertidal oyster reefs using a dip net (1.6 mm mesh; 40 cm x 23 cm frame), sacrificed by cervical dislocation, and stored at -15°C until laboratory analyses. A maximum of 12 fish of both species were collected on each sampling date.

Adult fish morphological data. Fishes were thawed before laboratory processing. Standard length (SL, mm), measured as the distance from the snout to the distal end of the caudal peduncle, was recorded for all naked gobies and striped blennies collected from June 2012 through December 2013. Body depth (BD, mm), measured as the straight line distance from the anterior edge of the dorsal fin to the ventral surface, was recorded for naked gobies and striped blennies collected from September through December 2013. Whole fish wet tissue weight (WTW, g) was measured to the nearest 0.001 g for all fishes.

Gonadal tissue, consisting of both ovaries (females) and both testes (males), was separated from all somatic tissue. Somatic and gonad wet tissue weights were measured to the nearest 0.001 g. All fish tissues were dried at 80°C for 72 hours (or until constant weight) to obtain dry tissue weight (DTW, 0.001 g). Whole fish DTW was calculated by adding somatic and gonadal DTW.

Fish sex was determined using body morphology and gonad color and texture. Striped blenny males and females were distinguished by coloration patterns (Fritzsche 1978; Able and Fahay 1998). Males had horizontal brown and yellow stripes along their sides of their bodies. Blue spots were present at the anterior tip of male dorsal fins during the spawning season. Female blennies had brown cross-bar patterns and multiple pale white blotches along their sides. Naked goby males and females were distinguishable by the shape of the genital papilla (Dahlberg and Conyers 1973). Naked goby and striped blenny testes were distinguished from ovaries by shape (long, thin, and cylindrical) and color (white; Hildebrand and Cable 1938; Miller 1984). Female ovaries were pale yellow to deep orange for both species (Hildebrand and Cable 1938; Nero 1976; Miller 1984). Ovaries were identified as gravid based on the presence of oocytes (per Lowerre-Barbieri et al. 1996; White et al. 2003; Murua et al. 2003). Fishes were characterized as "indeterminate" if no gonad was observed.

A gonadosomatic Index (GSI) was calculated for each fish with identifiable gonads using the equation from Zucchetta et al. (2012):

$$\text{GSI (\%)} = \frac{\text{gonad WTW (g)}}{\text{whole fish WTW (g)}} \times 100$$

An ovary subsample was taken from gravid females containing greater than 20 oocytes, or 5% of gonadal tissue, depending on gonad size. Gonad subsample WTW (0.001 g) was measured and the number of oocytes within the subsample was counted. The number of oocytes female^{-1} was calculated per Way et al. (1998):

$$\text{Weight of one oocyte (g)} = \frac{\text{Number of oocytes subsample}^{-1}}{\text{Gonad subsample WTW (g)}}$$

$$\text{Number of oocytes female}^{-1} = \frac{\text{Total gonad WTW (g)}}{\text{weight of one oocyte (g)}}$$

An index of female reproductive condition (FRC) was calculated to standardize comparisons between females of different lengths using the equation from Way et al. (1998):

$$\text{FRC} = \frac{\text{gonad WTW (g)}}{\text{fish standard length (mm)}} \times 100$$

Oocyte diameters (mm) were measured for 60 oocytes within the ovaries of each gravid female. Ten oocytes were taken from the anterior, middle, and posterior sections of both the right and left ovaries.

Data analyses. Significance levels for all statistical tests were established *a priori* at alpha = 0.05. Assumptions of homogeneity of variance were tested using Levene's test and assumptions of normality were tested with the Shapiro-Wilks test (Zar 2010). Data satisfied these assumptions unless otherwise indicated. Post-hoc multiple comparisons were made with Tukey's (parametric) or Dunn's (non-parametric) test when needed (Zar 2010).

Morphological relationships. Adult naked goby and striped blenny standard length (SL, mm), whole fish WTW (g), and whole fish DTW (g) frequency distributions were described by sampling week. Linear regressions were used to describe relationships between fish SL (mm), or BD (mm), and whole fish WTW (g) and whole fish DTW (g) using the equation:

$$\text{Y} = \text{m (X)} + \text{b}$$

Where Y equals body depth or whole fish WTW, b equals the y-axis intercept, m equals the slope, and X equals SL or whole fish DTW. T-tests were used to test for differences (Zar 2010) between the slopes of the lines for male and female SL- BD and whole fish WTW-whole fish DTW relationships. The relationships between SL and BD and whole fish WTW and whole fish DTW were not significantly different between males and females for either species (Appendix 1 and 2). Thus, SL-BD and whole fish WTW-whole fish DTW relationships are presented with male and female data combined.

The percentage of water lost after drying was calculated for naked goby and striped blenny adults using the equation:

$$\text{Percent water loss (\%)}= \frac{\left(\text{whole fish WTW (g)-whole fish DTW (g)}\right)}{\text{whole fish WTW (g)}}\text{ x 100}$$

A power equation was used to describe the relationships between fish SL (mm) and whole fish WTW (g) and whole fish DTW (g):

$$\mathrm{Y}=a(\mathrm{X})^{b}$$

where Y equals whole fish WTW or DTW, *a* equals minimum SL, X equals SL, and *b* describes the steepness of the curve. Standard length and weight data were logarithm transformed prior to analyses with t-test (Zar 2010). The relationships between SL and weight were significantly different in males and females of both species (Appendix 1 and 2). Thus, SL-weight relationships are presented by species and sex.

Gonadosomatic indices. Pearson correlations were used to describe the relationships between male and female naked goby and striped blenny, average water temperature (°C) and day-length (hr) corresponding to the time intervals between fish collections and naked goby and striped blenny GSI (%) values. Cumulative day-degree (CumD) values were calculated for naked gobies and striped blennies in 2012 and 2013 using the equation proposed by Wilson and Simons (1985):

$$\mathrm{D} = \sum_{n=i}^{n} (t_i - t_0)$$

where D is the day-degree temperature coefficient, t_i equals the average daily water temperature (°C) recorded in Crabhaul Creek, North Inlet from January 1 through the last day of the spawning season, and t_0 equals the estimated water temperature for the initiation of gonad development. The water temperature for the initiation of fish gonad development was estimated to be 10°C (Dawson 1966; Nero 1976). CumD values were calculated for the observed onset and end of spawning in North Inlet for both species in 2012 and 2013 and compared to predicted CumD values based on an 18°C threshold for the onset of spawning (Dawson 1966). Pearson correlations were used to describe relationships between cumulative day degree values on the day of collection and male and female naked goby and striped blenny GSI (%) values.

Oocyte diameter and female morphological relationships. Individual two-way ANOVAs were used to test for differences in oocyte diameters between anterior, middle, and posterior sections of both the right and left lobes and between the right and left lobes for naked goby and striped blenny females. Box whisker plots were used to describe oocyte diameter ranges for individual gravid females by collection week. Oocyte diameters (mm) were standardized by fish SL (mm) to remove oocyte diameter variability attributed to female size.

The relationships between female SL (mm), BD (mm), gonad WTW (g), and whole fish WTW (g) and the number of oocytes female^{-1} were described with the power equation (presented above) where Y equals the number of oocytes female^{-1}, *a* equals the minimum number of oocytes female $^{-1}$, *b* describes the steepness of the curve, and X equals SL, BD, gonad WTW, or whole fish WTW. The power model was also used to describe the relationships between gonad WTW (g) and female SL (mm), BD (mm), and whole fish WTW (g).

RESULTS

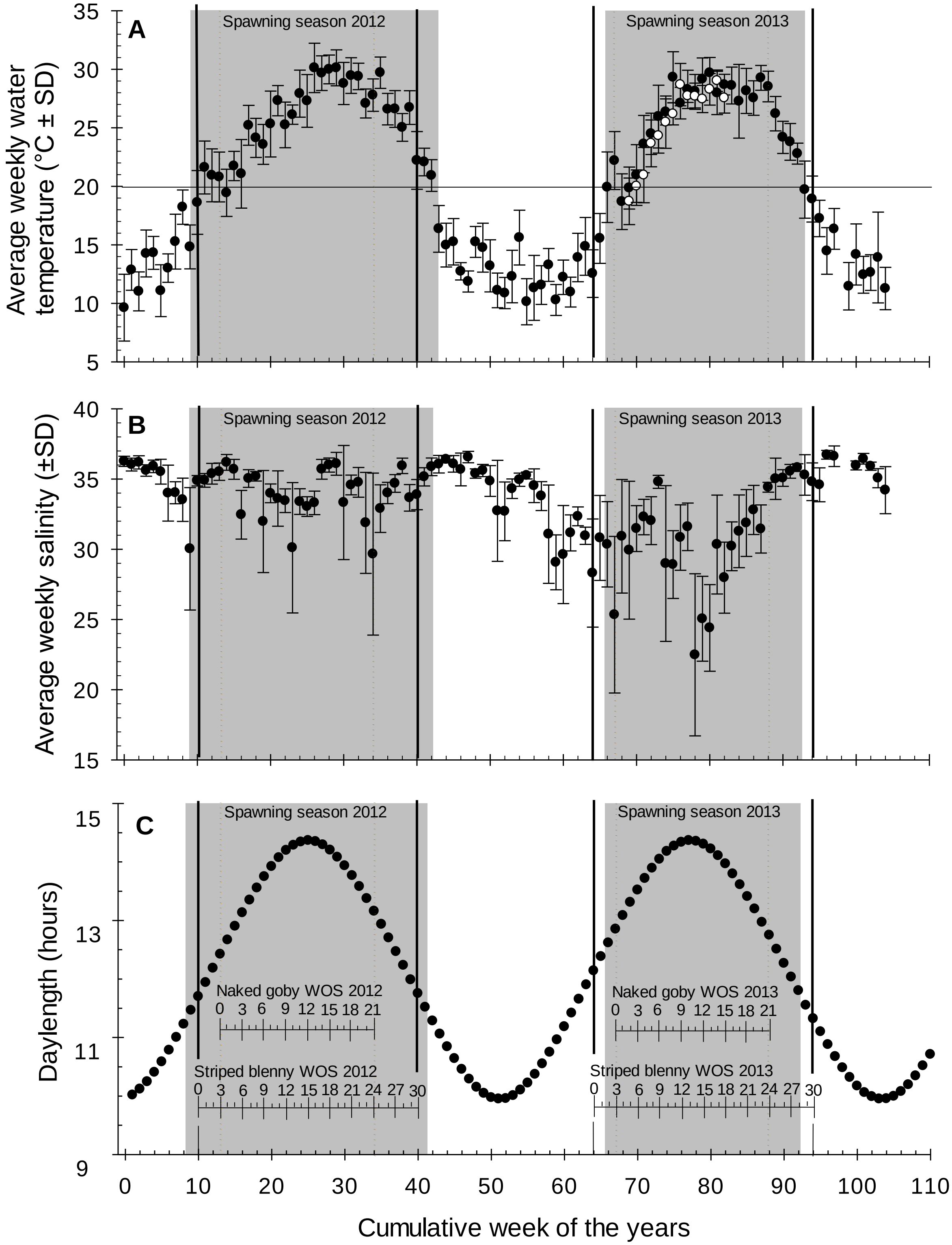
Environmental conditions. North Inlet water temperatures (WT) typically range between 3°C and 36°C (Allen et al. 2008). Winter (December-February) and summer (June-August) median WT were 10°C and 27°C, respectively during 1981-2006 (Allen et al. 2008). Average WT during spring was 21.9 ± 3.3°C in 2012 compared to 18.7 ± 4.8°C in 2013 (Figure 3A). Winter (December-February), summer (June-August) and fall (September-November) WT were approximately 13°C, 28°C and 20°C, respectively, for both years (Figure 3A).

North Inlet salinities typically range between 5 and 38 (Allen et al. 2008). In 2013, salinity ranged between 22.5 and 36.7 with an average of 34.5±0.7 during 2012 and 32.1±1.4 during 2013 (Figure 3B). Winter salinity in 2013 was 2 units lower than in 2012. Spring and summer salinities in 2013 were 4 units lower than the observed salinities in 2012 (Figure 3B). A period of lowered salinity was observed during the naked goby and striped blenny 2013 spawning seasons from March 17 (CumWOY 63) to July 28 (CumWOY 82) due to rainstorms (Figure 3B).

Day-length during the naked goby and striped blenny spawning seasons ranged between 11.8 and 14.5 hr (Figure 3C). Naked goby spawning began after day-length exceeded 12.5 hours and continued until day-length fell below 13 hr. Striped blenny spawning began when day-length exceeded 11.2 hr and continued until day-length fell below 12 hr.

Spawning season duration and nest observations. The naked goby spawning season lasted for 21 weeks in both 2012 and 2013 (Figure 3; Appendices 3 and 4). Naked goby nests were first observed between April 5-15 (2012: 21°C; 2013: 22°C) and last observed

Figure 3: Average weekly (A) water temperature (°C) and (B) salinity (cdmo.baruch.sc.edu) with standard deviation and (C) day-length (hr; usno.navy.mil) observed at Crabhaul Creek (closed circles) in North Inlet, SC and for laboratory culture flumes (open circles) from January 1, 2013 through December 31, 2013. Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period. Spawning season duration (grey boxes) was predicted using water temperature thresholds of 18°C (horizontal line). Naked goby and striped blenny observed weeks of the spawning season (WOS) are indicated by the inset axes. The onset and end of the spawning seasons are indicated by dashed (goby) and solid (blenny) vertical lines.


A
B
C
Spawning season 2012
Spawning season 2013
Average weekly water temperature (°C ± SD)
Average weekly salinity (±SD)
Daylength (hours)
Naked goby WOS 2012
Naked goby WOS 2013
Striped blenny WOS 2012
Striped blenny WOS 2013
Cumulative week of the years

between September 1-6 (28°C both years). At least one naked goby nest was observed during the majority (80%) of bi-weekly spawning season sampling dates (Figure 4A).

The striped blenny spawning season began three weeks earlier than the naked goby spawning season and at lower water temperatures. The striped blenny spawning season lasted for 30 weeks in both years (Figure 3; Appendices 3 and 4). Striped blenny nests were first observed during the third week of March (2012: 19°C; 2013: 13°C) and last observed the first week of October (2012: 22°C; 2013: 19°C). At least two striped blenny nests were observed during the majority (85%) of bi-weekly sampling dates during the spawning seasons (Figure 4B).

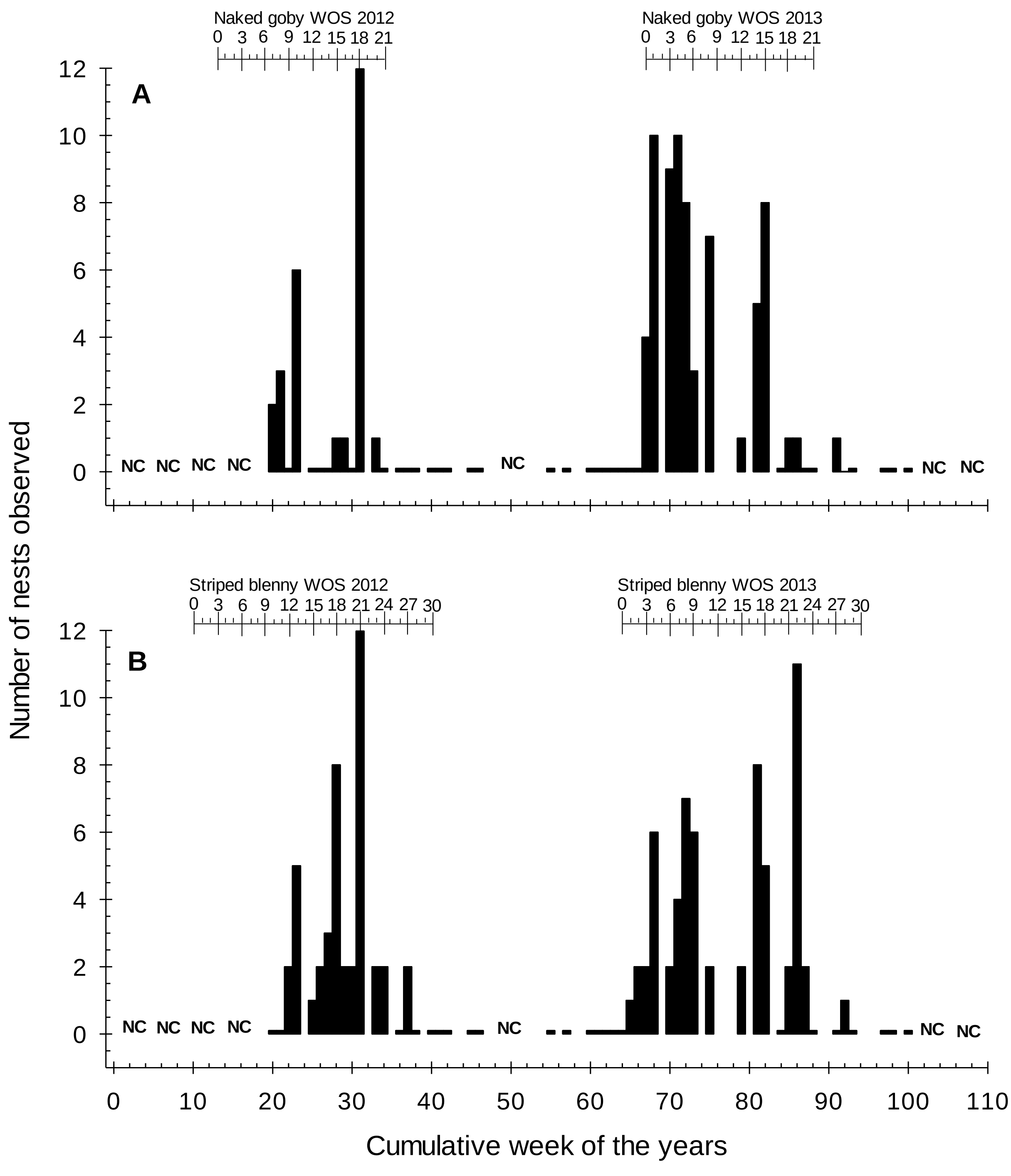
The absence of nest observations within a week should not be interpreted as the absence of fish spawning. Rather, the lack of observations is due to the observation methods. Fish nests could not be observed in water depths > 1 m.

Cumulative day-degrees. Naked gobies spawned at warmer water temperatures than predicted by the literature (e.g., Dawson 1966; Dahlberg and Conyers 1973). Observed cumulative day-degree (CumD) values were higher than those calculated with predicted spawning temperature thresholds of 18°C (Table 2). Striped blennies spawned at water temperatures below what would be expected in 2013 (13°C). Observed CumD values for striped blennies were lower in 2013 (Table 2). Fish are mobile, and although the weekly water temperature was below the 18°C spawning temperature thresholds, striped blennies likely moved to shallow areas that experience water temperatures above the observed average. In the fall, both the naked goby and striped blenny ceased spawning before water temperatures declined below 18°C. Observed CumD values were lower than those calculated using spawning temperature 18°C spawning temperature thresholds (Table 2).

Table 2: Cumulative day-degree (CumD) estimates for the start and end dates of the naked goby and striped blenny spawning seasons for 2012 and 2013 using nest observations and the predicted onset threshold of 18°C. Predicted CumD estimates using the 18°C spawning temperature threshold are presented in parentheses. Cumulative week of the years (CumWOY) corresponds to the sampling week within the study period.

Species	Year	Start date	Cum WOY	Start CumD	End date	Cum WOY	End CumD
Naked goby	2012	04/05/12 (02/24/12)	13 (7)	510 (148)	09/01/12 (10/30/12)	34 (43)	2954 (2706)
	2013	04/14/12 (04/08/13)	67 (66)	327 (263)	09/02/13 (10/25/13)	88 (94)	2610 (3392)
Striped blenny	2012	3/18/12 (02/24/12)	10 (7)	304 (148)	10/06/12 (10/30/12)	40 (43)	3547 (3817)
	2013	3/30/13 (04/08/13)	64 (66)	209 (263)	10/14/13 (10/25/13)	94 (94)	3265 (3392)

Figure 4: The number of nests observed for (A) naked gobies and (B) striped blennies during nest surveys on North Inlet, SC oyster reefs from June 2012 (CumWOY 20) through December 2013 (CumWOY 100). A zero value indicates weeks when observations were made but no fish nests were observed. NC (no collection) indicates weeks that no observations were made. Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period. Weeks of the spawning season (WOS) are indicated by the inset axes.



Naked goby WOS 2012
0 3 6 9 12 15 18 21
Naked goby WOS 2013
0 3 6 9 12 15 18 21
A
NC
Striped blenny WOS 2012
0 3 6 9 12 15 18 21 24 27 30
Striped blenny WOS 2013
0 3 6 9 12 15 18 21 24 27 30
B
Number of nests observed
Cumulative week of the years

Morphological relationships. A total of 122 naked gobies and 116 striped blennies were collected from June 2012 through December 2013 (Figure 5). Male, female, and indeterminate fishes composed 70%, 11%, and 19% (goby; Figure 6) and 60%, 37%, and 3% (blenny; Figure 7) of the total collection. Observed sex ratios were 4:1 and 2:1 for naked gobies and striped blennies, respectively.

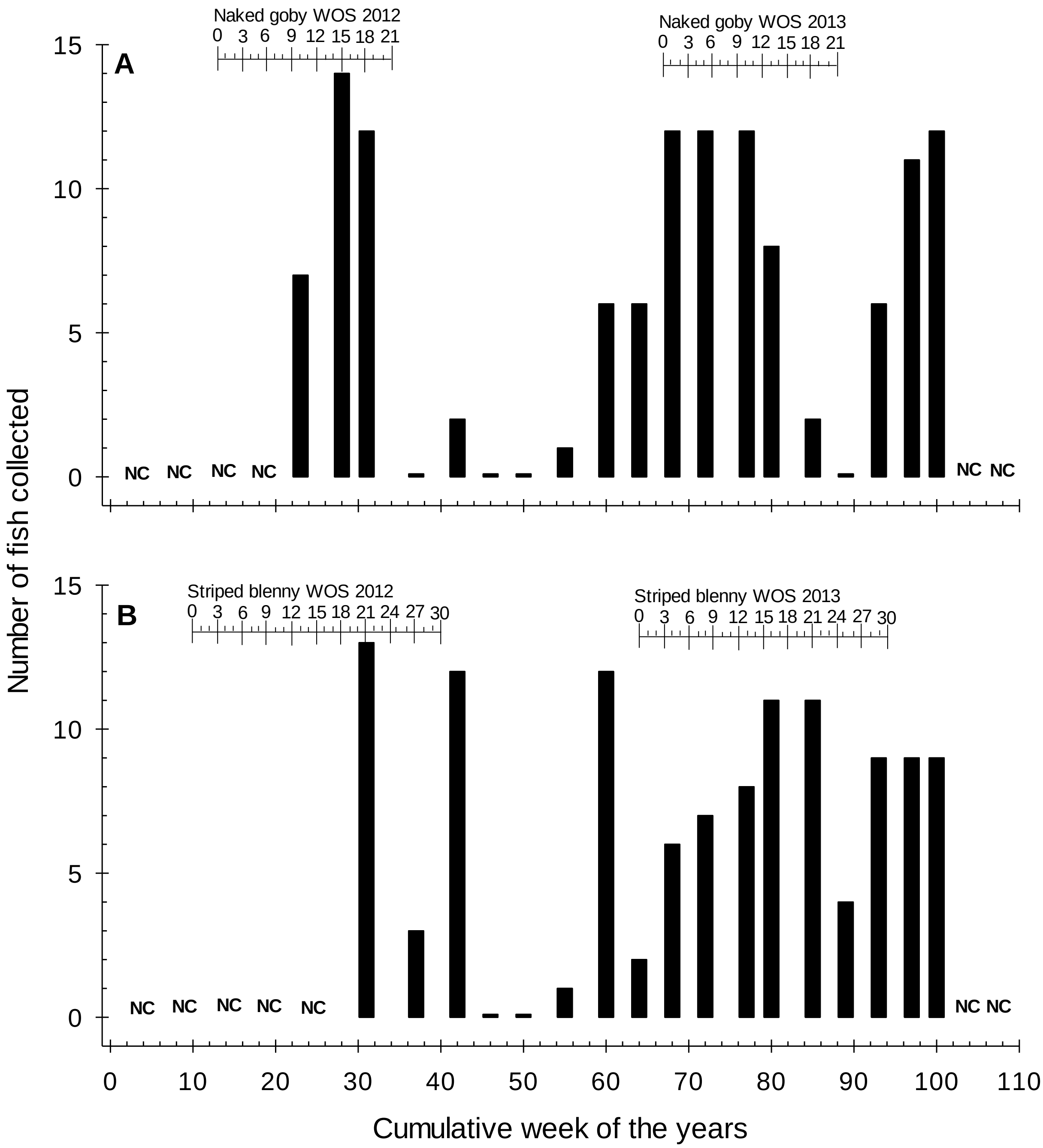
Standard length. Naked goby males (n = 85) were between 20-60 mm SL (Table 3; Figure 8A; Appendix 5). The majority of males (66%) were > 35 mm SL. The largest males (50-60 mm SL, n = 6) were observed only during weeks 0-6 of the 2013 spawning season (Figure 8A). The smallest naked goby males (20-25 mm SL) were collected during week 15 of the 2012 spawning season and the first week of the 2013 spawning season (Figure 8A). Naked goby females (n = 14) were 20-45 mm SL (Table 3; Figure 8A; Appendix 6). The majority of females (57%) were between 30-40 mm SL. Indeterminate naked gobies (< 36 mm SL, n = 23; Table 3; Figure 8A; Appendix 7) were collected between weeks 10-18 of the naked goby spawning season in 2012, but only before the first week and after the last week of the naked goby spawning season in 2013. The absence of larger males later in the spawning season suggests migration into deeper habitats, or possibly, mortality (Hildebrand and Cable 1938; Nero 1976). Naked goby lifespan estimates are 1-2 years (Hildebrand and Cable 1938; Nero 1976). The appearance of smaller naked gobies at the end of the spawning season indicates the growth of the young of the year individuals produced at the beginning of the spawning season.

Striped blenny males (n = 70) were 25-70 mm SL (Table 3; Figure 8B; Appendix 8). The majority of striped blenny males (74%) were > 50 mm SL. Smaller males (< 40

Table 3: Standard length (SL, mm) frequency distribution for naked gobies and striped blennies collected from North Inlet, SC oyster reefs from June 2012 through December 2013. The number of fish examined by 5 mm standard length bins, sex, and species is presented.

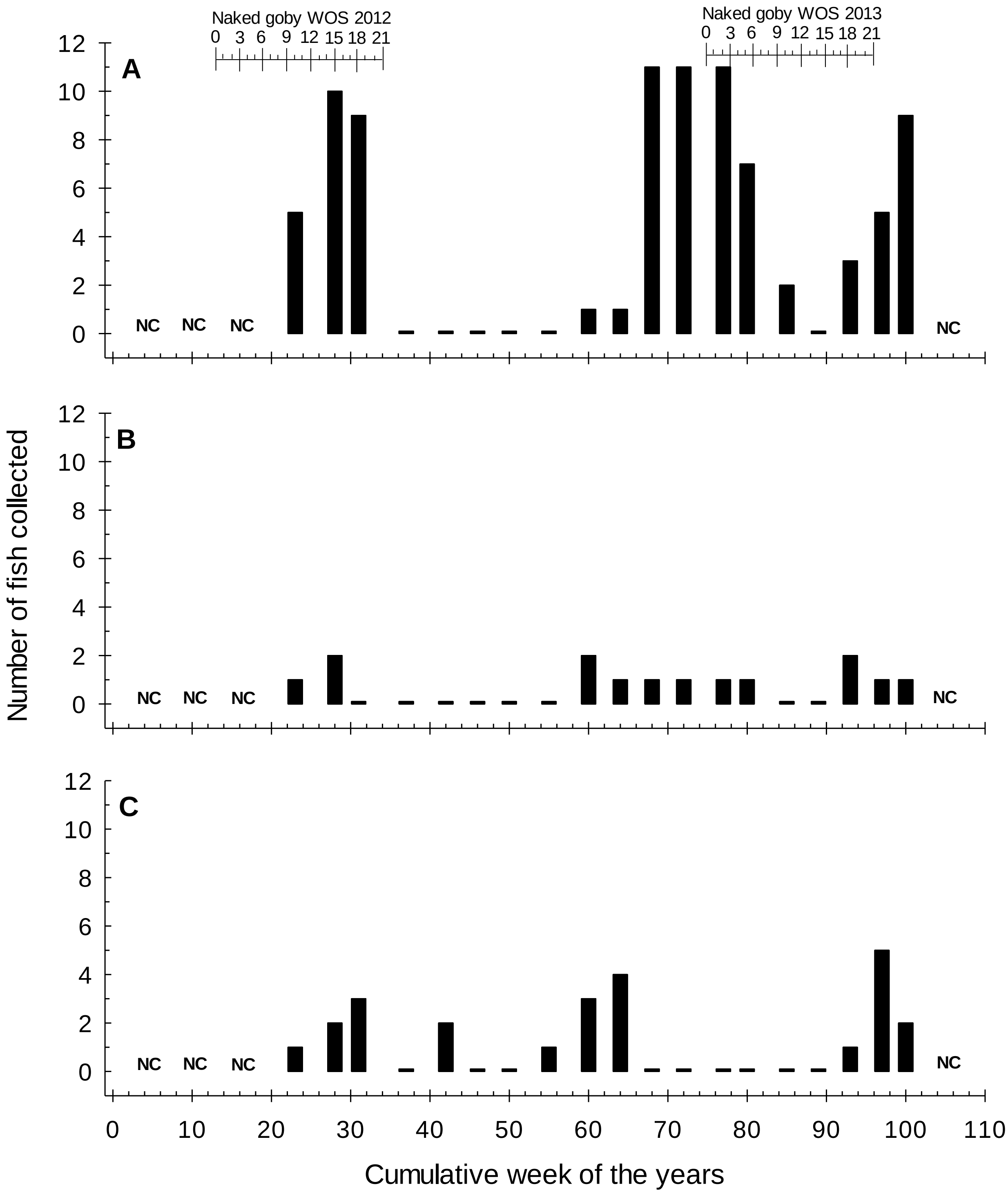
Species	Standard length bin (mm) 15.0-19.9	20.0-24.9	25.0-29.9	30.0-34.9	35.0-39.9	40.0-44.9	45.0-49.9	50.0-54.9	55.0-59.9	60.0-64.9	65.0-69.9
Naked goby											
Male	0	6	13	10	15	16	19	5	1	0	0
Female	0	2	3	4	4	1	0	0	0	0	0
Indeterminate	3	12	5	2	1	0	0	0	0	0	0
Total	**3**	**21**	**21**	**16**	**20**	**17**	**19**	**5**	**1**	**0**	**0**
Striped blenny											
Male	0	0	3	2	3	7	3	19	16	16	1
Female	0	0	4	5	5	7	10	5	6	0	0
Indeterminate	0	1	2	1	0	0	0	0	0	0	0
Total	**0**	**1**	**9**	**8**	**8**	**14**	**13**	**24**	**22**	**16**	**1**

Figure 5: The number of naked gobies (A, n = 122) striped blennies (B, n = 116) collected from North Inlet, SC oyster reefs from June 2012 (CumWOY 22) through December 2013 (CumWOY 100). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period. A zero value indicates sampling weeks when no fish were collected. NC (no collection) indicates weeks when no collections were made. Weeks of the spawning season (WOS) are indicated by the inset axes.



Naked goby WOS 2012
0 3 6 9 12 15 18 21
Naked goby WOS 2013
0 3 6 9 12 15 18 21
A
NC NC NC NC
NC NC
Striped blenny WOS 2012
0 3 6 9 12 15 18 21 24 27 30
Striped blenny WOS 2013
0 3 6 9 12 15 18 21 24 27 30
B
NC NC NC NC NC
NC NC
0
5
10
15
0 10 20 30 40 50 60 70 80 90 100 110
Number of fish collected
Cumulative week of the years

Figure 6: The number of male (A, n = 84), female (B, n = 14), and indeterminate (C, n = 23) naked gobies collected from North Inlet, SC oyster reefs from June 2012 (Cum WOY 22) through December 2013 (CumWOY 100). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period. A zero value indicates sampling weeks when zero fish were collected. NC (no collection) indicates weeks when no collections were made. Weeks of the spawning season (WOS) are indicated by the inset axes.



Naked goby WOS 2012
0 3 6 9 12 15 18 21
Naked goby WOS 2013
0 3 6 9 12 15 18 21
A
B
C
NC
Number of fish collected
Cumulative week of the years
0 10 20 30 40 50 60 70 80 90 100 110
0 2 4 6 8 10 12

Figure 7: The number of male (A, n = 70), female (B, n = 42), and indeterminate (C, n = 4) striped blennies collected from North Inlet, SC oyster reefs from August 2012 (CumWOY 30) through December 2013 (CumWOY 100). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period. A zero value indicates sampling weeks when zero fish were collected. NC (no collection) indicates when no collections were made. Weeks of the spawning season (WOS) are indicated by the inset axes.

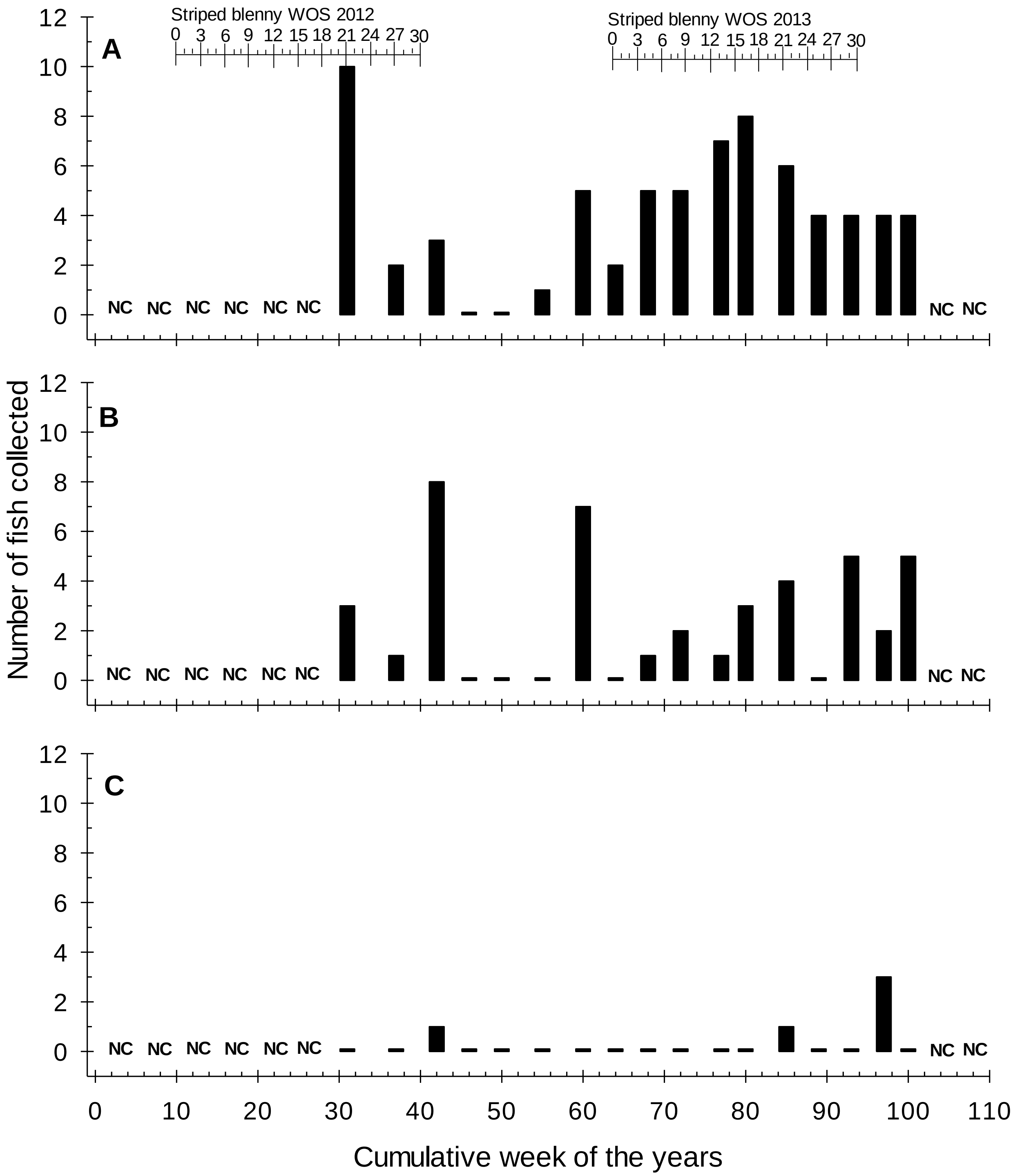
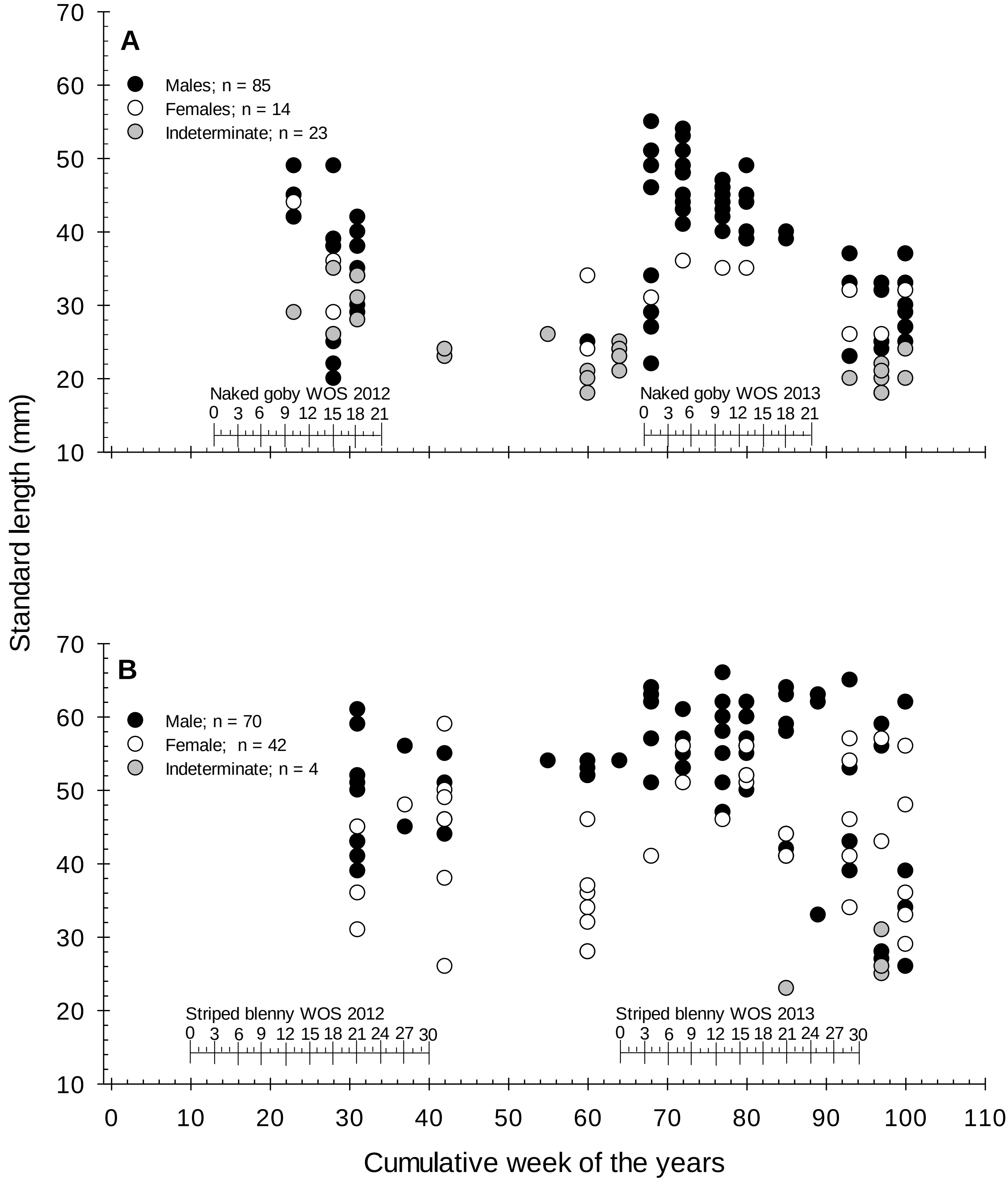

Striped blenny WOS 2012
Striped blenny WOS 2013
A
B
C
NC
Number of fish collected
Cumulative week of the years

Figure 8: Naked goby (A, n = 122) and striped blenny (B, n = 116) standard length (mm) by sampling week collections from June 2012 (CumWOY 23) through December 2013 (CumWOY 100). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period. Weeks of the spawning season (WOS) are indicated by the inset axes.


A
Males; n = 85
Females; n = 14
Indeterminate; n = 23
Naked goby WOS 2012
0 3 6 9 12 15 18 21
Naked goby WOS 2013
0 3 6 9 12 15 18 21
B
Male; n = 70
Female; n = 42
Indeterminate; n = 4
Striped blenny WOS 2012
0 3 6 9 12 15 18 21 24 27 30
Striped blenny WOS 2013
0 3 6 9 12 15 18 21 24 27 30
Standard length (mm)
10
20
30
40
50
60
70
Cumulative week of the years
0 10 20 30 40 50 60 70 80 90 100 110

mm SL) were collected only after week 20 of the spawning season in both years. The smallest males (25-30 mm SL) were collected after the end of the 2013 spawning season (Table 3; Figure 8B). Blenny females (n = 42) were 25-60 mm SL (Table 3; Figure 8B; Appendix 9). Half of the females were > 45 mm SL (Table 3). All of the indeterminate striped blennies (< 35 mm SL; n = 4) except one were collected after the end of the spawning season in November 2013 (Table 3; Figure 7C and Figure 8B; Appendix 10).

The observed male and female naked goby standard length ranges were on the upper end of values previously reported (Table 1). The observed male striped blenny standard length range was lower than the range previously reported for North Inlet, but within the ranges reported for the Chesapeake Bay and North Carolina (Table 1). The observed female striped blenny standard length range was within the previously reported range for North Carolina (Table 1).

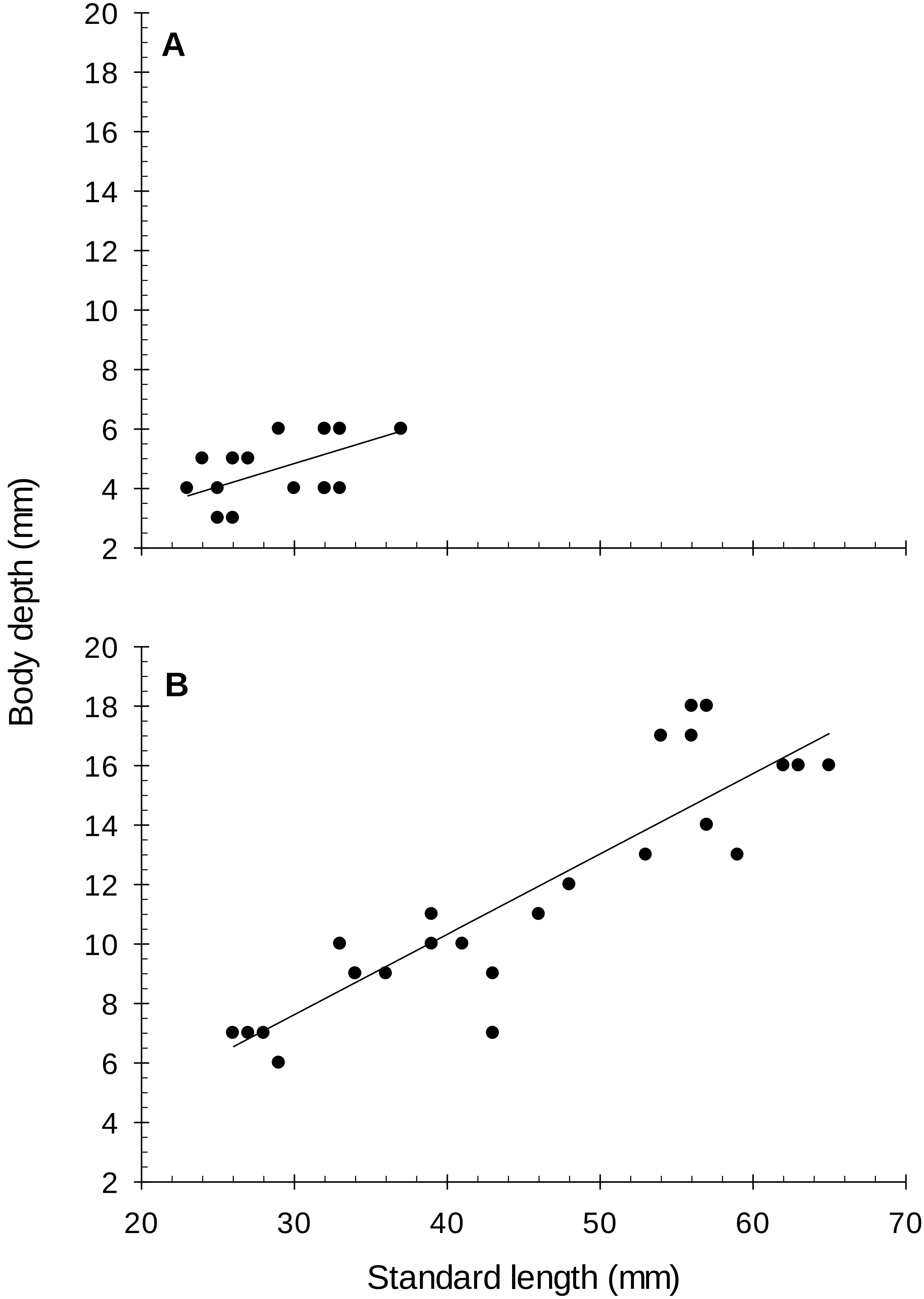
Blennies were generally longer than gobies. The naked goby and striped blenny male SL demographic overlapped between 25 mm and 60 mm SL. Ninety-three percent of naked goby males and 76% of striped blenny males were within this common range. The naked goby and striped blenny female SL demographic overlapped between 25 and 45 mm SL. Eighty-eight percent of naked goby females and 50% of striped blenny females were within this common range.

Standard length- body depth. Body depth scaled proportionately with SL for both naked gobies (R^2 = 0.39, n = 25) and striped blennies (R^2 = 81, n = 28; Table 4; Figure 9). Naked gobies in this relationship represent the lower half (20-40 mm SL) of the observed SL range. Since only 14 mm of the 45 mm range is represented, the lower R^2 value is expected for naked gobies. Predictions of body depth from SL should not be made

Table 4: Linear regression coefficients with (standard error) used to describe the relationships between standard length (SL, mm) and body depth (BD, mm) and between whole fish wet tissue weight (WTW, g) and whole fish dry tissue weight (DTW, g) in naked gobies and striped blennies. n equals the number of fish measured. b equals the y-axis intercept. m equals the slope. R^2 indicates how well the data fit the model.

Species	Relationship	n	b		m		R^2
Naked goby	WTW: DTW	99	0.02	(0.01)	0.19	(3.15)	0.91
	SL:BD	21	0.16	(1.35)	0.16	(0.05)	0.39
Striped blenny	WTW: DTW	112	0.03	(0.01)	0.22	(0.01)	0.96
	SL:BD	28	0.27	(0.03)	-0.42	(1.22)	0.81

Figure 9: The relationship between naked goby (A, n = 25, R^2 = 0.39) and striped blenny (B, n = 28, R^2 = 0.81) standard length (mm) and body depth (mm). Coefficients for the fitted linear regressions are presented in Table 4.


A
B
Body depth (mm)
Standard length (mm)
20
18
16
14
12
10
8
6
4
2
20
30
40
50
60
70

without including data from larger fishes. In contrast, the standard length-body depth relationship for striped blennies spans 85% of the observed SL range and includes representatives from the entire demographic. Thus, the standard length-body depth relationship can be used to predict body depth from standard length with 81% certainty. Within the common SL range (26-38 mm SL), striped blenny body depth was 3 mm greater than naked goby body depth for both males and females.

Whole fish wet and dry weight. Naked goby whole fish wet tissue weight (WTW) ranged between 0.087g and 3.172 g (Figure 10A). Goby whole fish dry tissue weight (DTW) ranged between 0.011 g and 0.644 g (Figure 11A). Male and female WTW and DTW were the greatest during weeks 1-6 of the 2013 spawning season when water temperatures were increasing from 20°C to 25°C (Figure 3A). By the end of the 2013 spawning season, male and female weights had decreased to two-thirds of the pre-spawning weight (Figure 10A and Figure 11A). These fish likely represent young of the year maturing into young adults.

Striped blennies were generally heavier than naked gobies. Striped blenny whole fish WTW ranged between 0.265 g and 5.935 g (Figure 10B). Blenny whole fish DTW (Figure 11B) ranged between 0.067 g and 1.424 g. Both male and female WTW and DTW were the greatest after week 24 of the spawning season. The heaviest fish likely represent the growth of already mature adults during the year. The lightest males and females present after week 24 of the spawning season likely represent young-of-the-year maturing into young adults. However, light fish may also represent adults that have recently spawned.

Figure 10: Naked goby (A, n = 122) and striped blenny (B, n = 116) whole fish wet tissue weight (g) for collections from June 2012 (CumWOY 23) through December 2013 (CumWOY 100). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period. Weeks of the spawning season (WOS) are indicated by the inset axes.

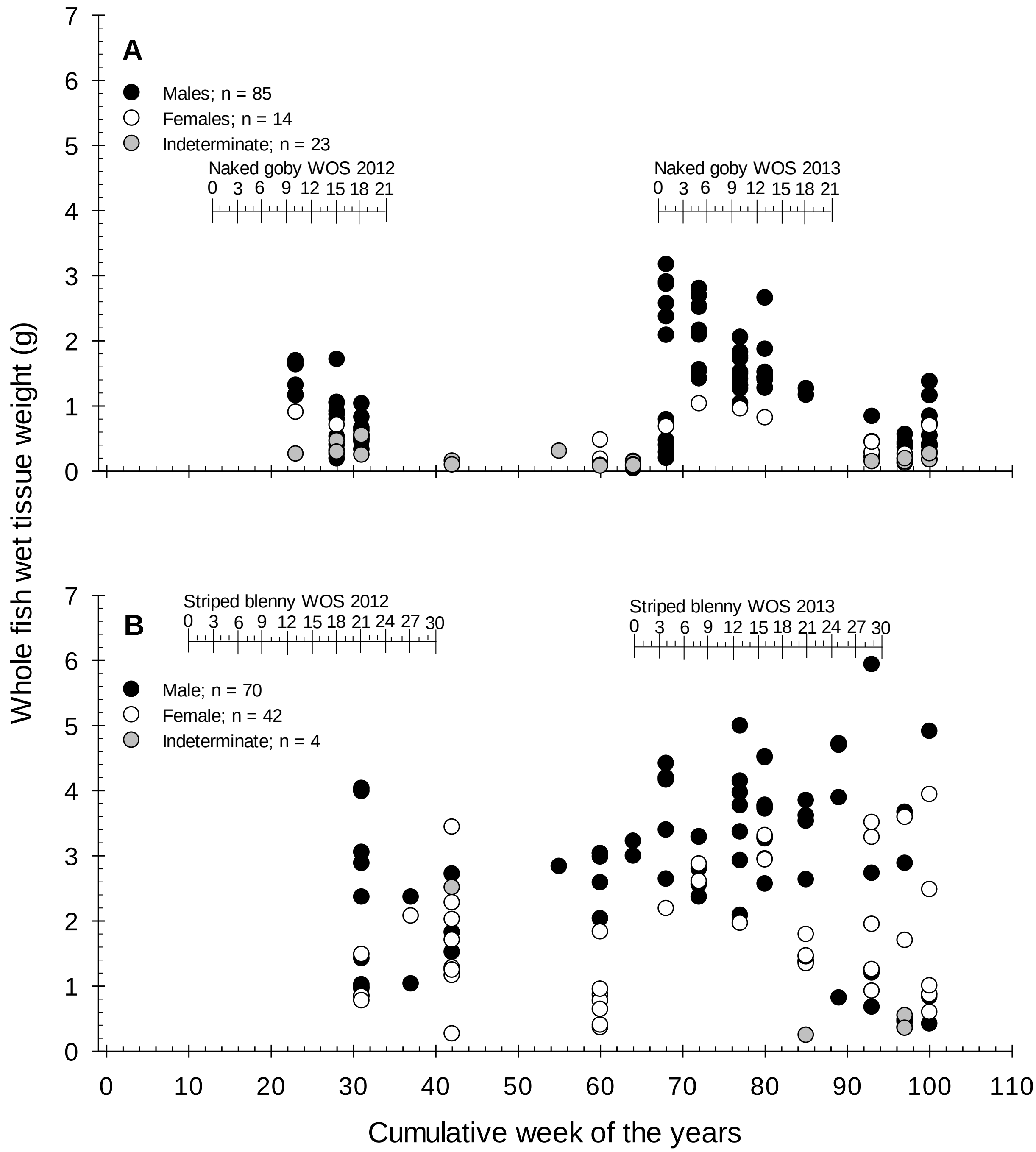
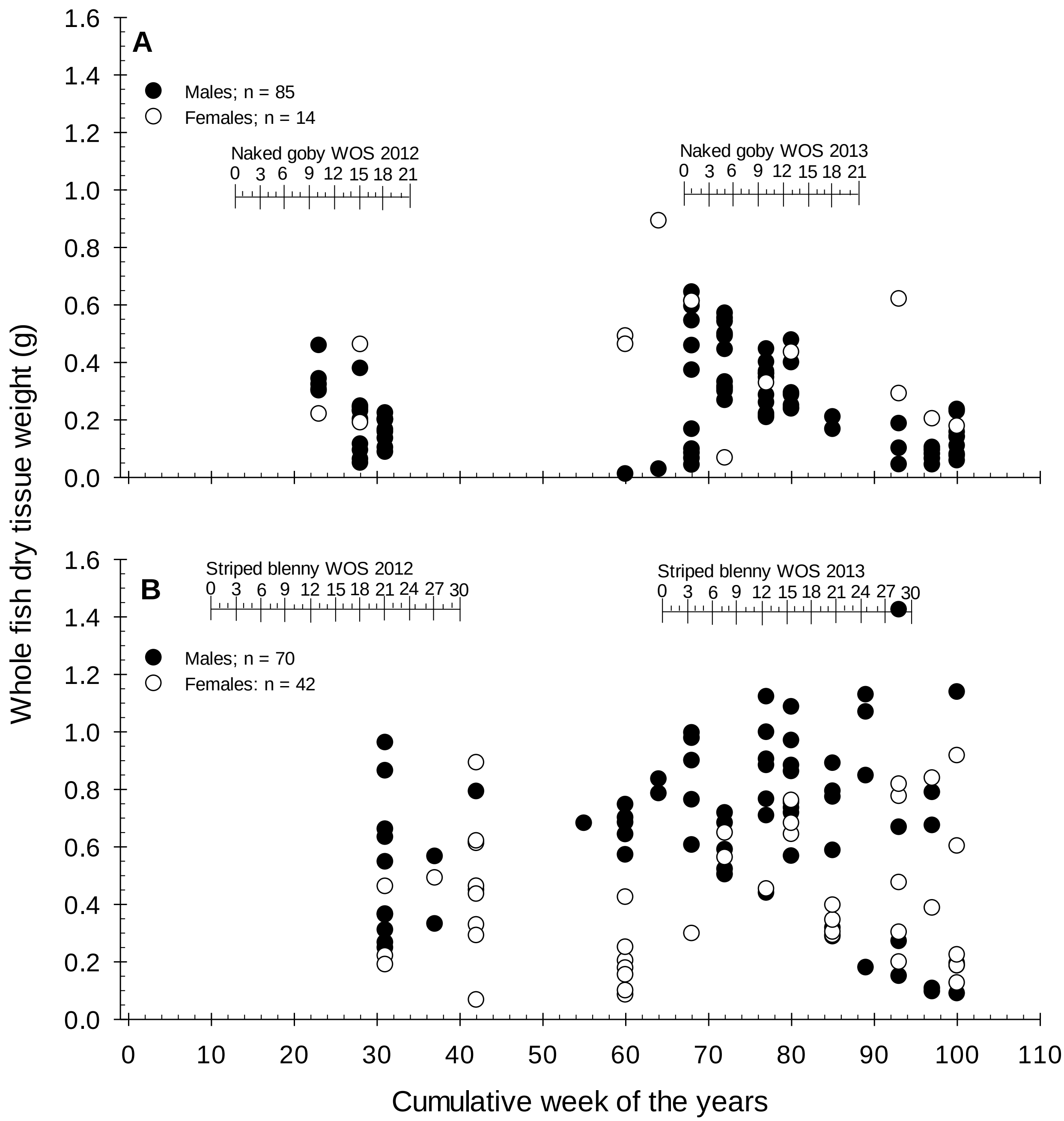

A
Males; n = 85
Females; n = 14
Indeterminate; n = 23
Naked goby WOS 2012
Naked goby WOS 2013
B
Striped blenny WOS 2012
Striped blenny WOS 2013
Male; n = 70
Female; n = 42
Indeterminate; n = 4
Whole fish wet tissue weight (g)
Cumulative week of the years

Figure 11: Naked goby (A, n = 99) and striped blenny (B, n = 112) whole fish dry tissue weight (g) from June 2012 (CumWOY 23) through December 2013 (CumWOY 100). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period. Weeks of the spawning season (WOS) are indicated by the inset axes.



Whole fish dry tissue weight (g)
A
Males; n = 85
Females; n = 14
Naked goby WOS 2012
0 3 6 9 12 15 18 21
Naked goby WOS 2013
0 3 6 9 12 15 18 21
B
Striped blenny WOS 2012
0 3 6 9 12 15 18 21 24 27 30
Striped blenny WOS 2013
0 3 6 9 12 15 18 21 24 27 30
Males; n = 70
Females: n = 42
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
0 10 20 30 40 50 60 70 80 90 100 110
Cumulative week of the years

Most male (61%, Figure 12A) and female (71%; Figure 13A) naked gobies lost 70-80% of their total body weight after drying. Median male (Figure 12C) and female (Figure 13C) gonadal tissue water loss was 80% during times of both spawning and non-spawning Naked goby whole fish DTW scaled proportionately with whole fish WTW (R^2 = 0.91; Table 4; Figure 14A).

Most male (94%; Figure 15A) and female (90%; Figure 16A) striped blennies lost 70-80% of their total body weight after drying. Median male (Figure 15C) and female (Figure 16C) gonadal tissue water loss (Figure 15C) was 80% during times of both spawning and non-spawning. Striped blenny whole fish DTW scaled proportionately with whole fish WTW (R^2 = 0.96; Table 4; Figure 14B)

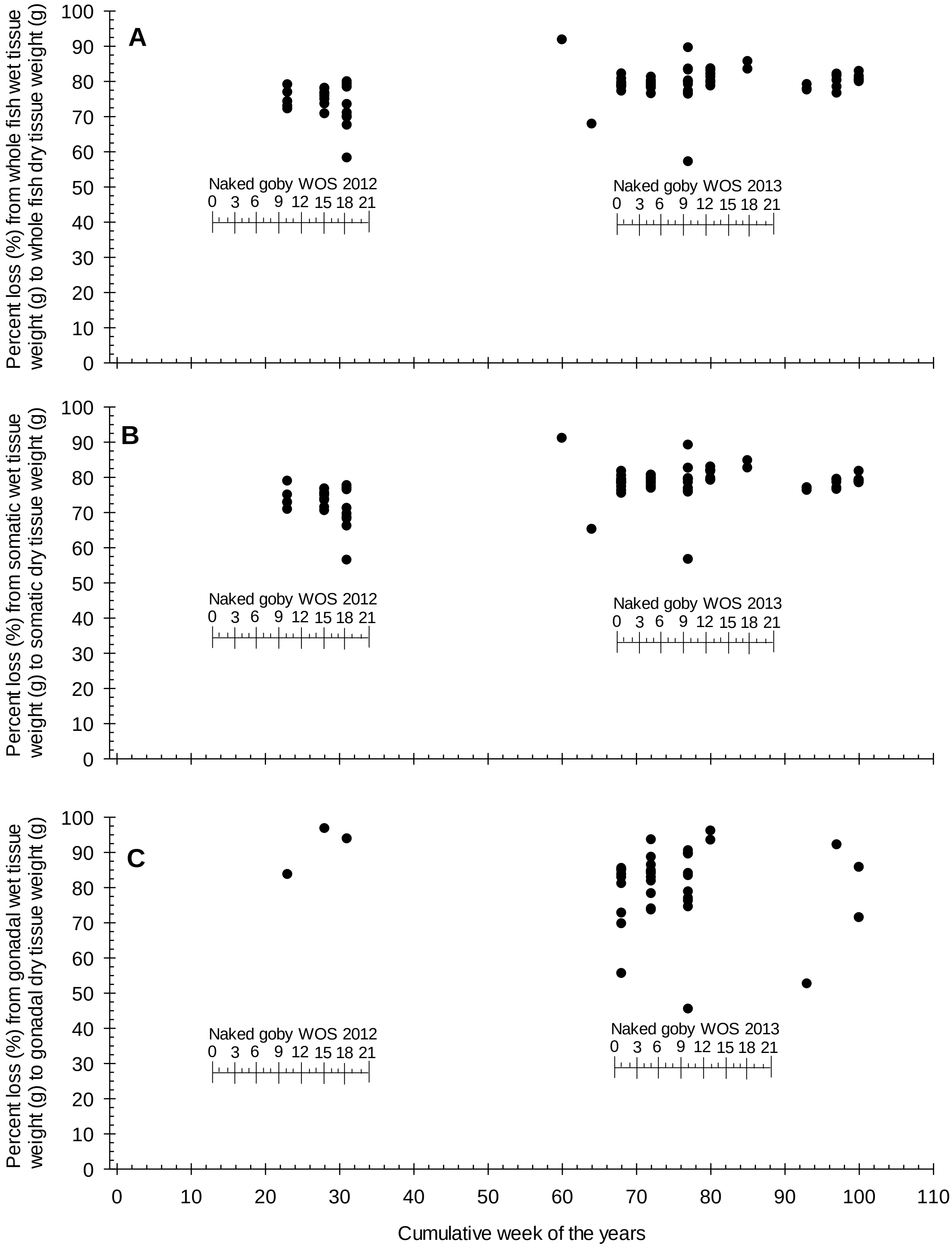
Standard length-weight relationships. Naked goby male (R^2 = 0.81, n = 85, Table 5; Figure 17A) and female (R^2 = 0.67, n = 14, Table 5; Figure 17B) whole fish WTW scaled non-linearly with SL. Naked goby male (R^2 = 0.80, n = 85, Table 5; Figure 18A) and female (R2 = 0.81, n = 14, Table 5; Figure 18B) whole fish DTW scaled non-linearly with SL. Male naked gobies (*b* =2.93) increased in weight at a faster rate than female naked gobies (*b* = 2.19, Table 5; Figure 17A and 17B).

Striped blenny male (R^2 = 0.88, n = 70, Table 5; Figure 17C) and female (R^2 = 0.88, n = 42, Table 5; Figure 17D) whole fish WTW scaled non-linearly with SL. Striped blenny male (R2 = 0.81, n = 70, Table 5; Figure 18C) and female (R2 = 0.81, n = 42, Table 5; Figure 18D) whole fish DTW scaled non-linearly with SL. Blenny WTW and DTW increased at a faster rate than SL. Male striped blennies (*b* = 2.92) increased weight at a faster rate than female striped blennies (*b* = 2.76, Table 5; Figure 17C and 17D).

Table 5: Power equation coefficients with (standard error) used to describe naked goby and striped blenny morphological relationships. The equation and model coefficients (a,b) are described in the text. SL equals standard length (mm). WTW equals wet tissue weight (g). DTW equals dry tissue weight (g). n equals the number of fish measured.

Species	Sex	Relationships	n	*a*		*b*		R^2
Naked goby	Male	SL: Whole fish WTW	85	$2.39x10^{-5}$	$(1.82x10^{-5})$	2.93	(0.20)	0.81
		SL: Whole fish DTW	85	$1.00x10^{-5}$	$(7.56x10^{-6})$	2.75	(0.20)	0.80
	Female	SL: Whole fish WTW	14	$2.84x10^{-4}$	$(5.04x10^{-4})$	2.19	(0.50)	0.67
		SL: Whole fish DTW	14	$2.64x10^{-5}$	$(3.48x10^{-5})$	2.47	(0.37)	0.81
Striped blenny	Male	SL: Whole fish WTW	70	$2.53x10^{-5}$	$(1.78x10^{-5})$	2.92	(0.17)	0.88
		SL: Whole fish DTW	70	$1.41x10^{-5}$	$(1.01x10^{-5})$	2.70	(0.18)	0.85
	Female	SL: Whole fish WTW	42	$4.83x10^{-5}$	$(3.72x10^{-5})$	2.76	(0.20)	0.88
		SL: Whole fish DTW	42	$1.02x10^{-5}$	$(6.66x10^{-6})$	2.80	(1.67)	0.91

Figure 12: Percent loss (%) from (A) whole fish, (B) somatic, and (C) gonadal wet tissue weight (g) to dry tissue weight (g) for male naked gobies (n = 85). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period from January 2012 (CumWOY 0) through December 2013 (CumWOY 100). Weeks of the spawning season (WOS) are indicated by the inset axes.



A
B
C
Percent loss (%) from whole fish wet tissue weight (g) to whole fish dry tissue weight (g)
Percent loss (%) from somatic wet tissue weight (g) to somatic dry tissue weight (g)
Percent loss (%) from gonadal wet tissue weight (g) to gonadal dry tissue weight (g)
Naked goby WOS 2012
Naked goby WOS 2013
0 3 6 9 12 15 18 21
0 10 20 30 40 50 60 70 80 90 100 110
Cumulative week of the years

Figure 13: Percent loss (%) from (A) whole fish, (B) somatic, and (C) gonadal wet tissue weight (g) to dry tissue weight (g) for female naked gobies (n = 14). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period from January 2012 (CumWOY 0) through December 2013 (CumWOY 100). Weeks of the spawning season (WOS) are indicated by the inset axes.

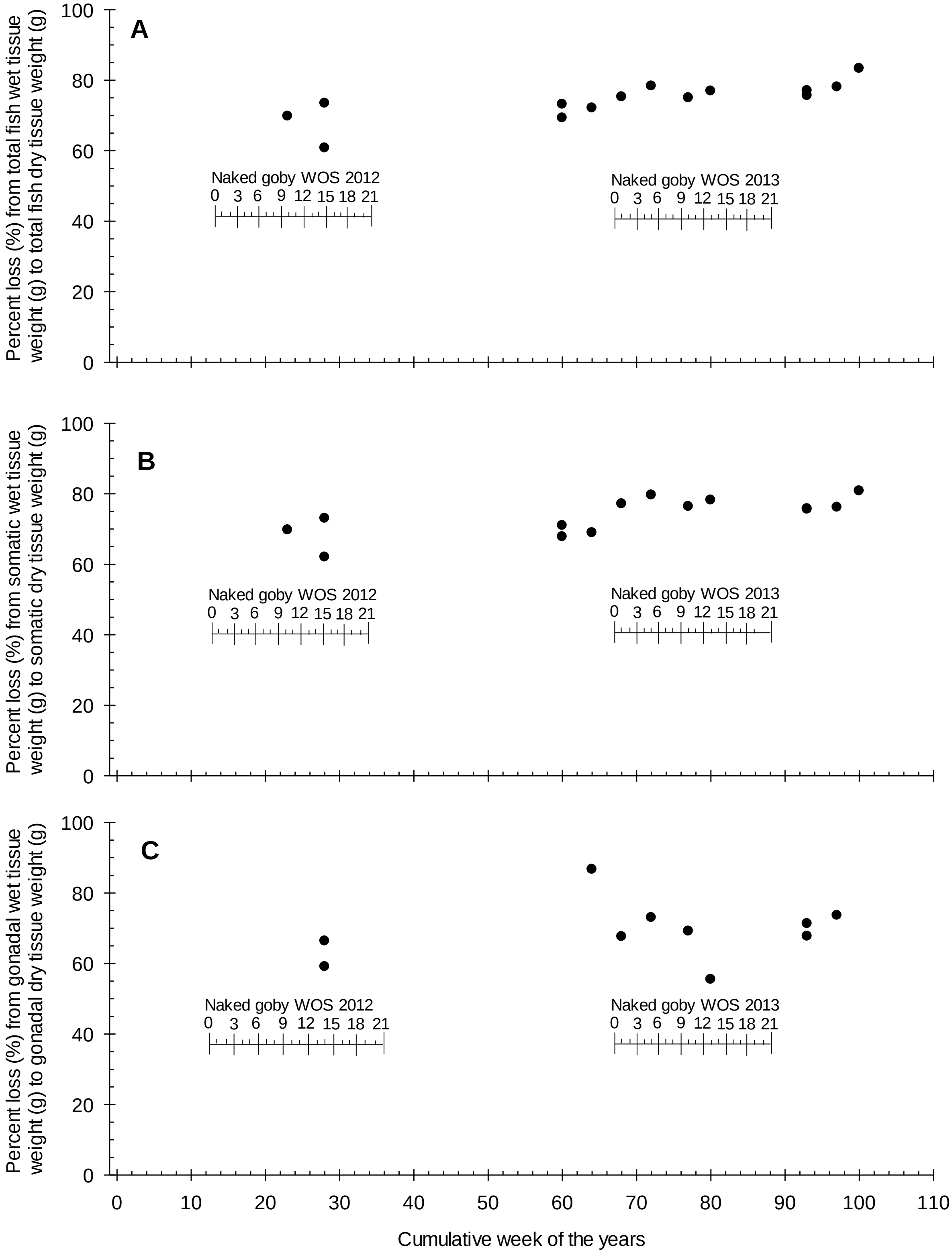

A
B
C
Naked goby WOS 2012
Naked goby WOS 2013
0 3 6 9 12 15 18 21
Percent loss (%) from total fish wet tissue weight (g) to total fish dry tissue weight (g)
Percent loss (%) from somatic wet tissue weight (g) to somatic dry tissue weight (g)
Percent loss (%) from gonadal wet tissue weight (g) to gonadal dry tissue weight (g)
Cumulative week of the years

Figure 14: The linear relationship between naked goby (A, n = 99, R^2 = 0.91, SL range 20-55 mm) and striped blenny (B, n = 112, R^2 = 0.96, SL range 26-66 mm) whole fish wet tissue weight (g) and whole fish dry tissue weight (g). Model coefficients are presented in Table 4.

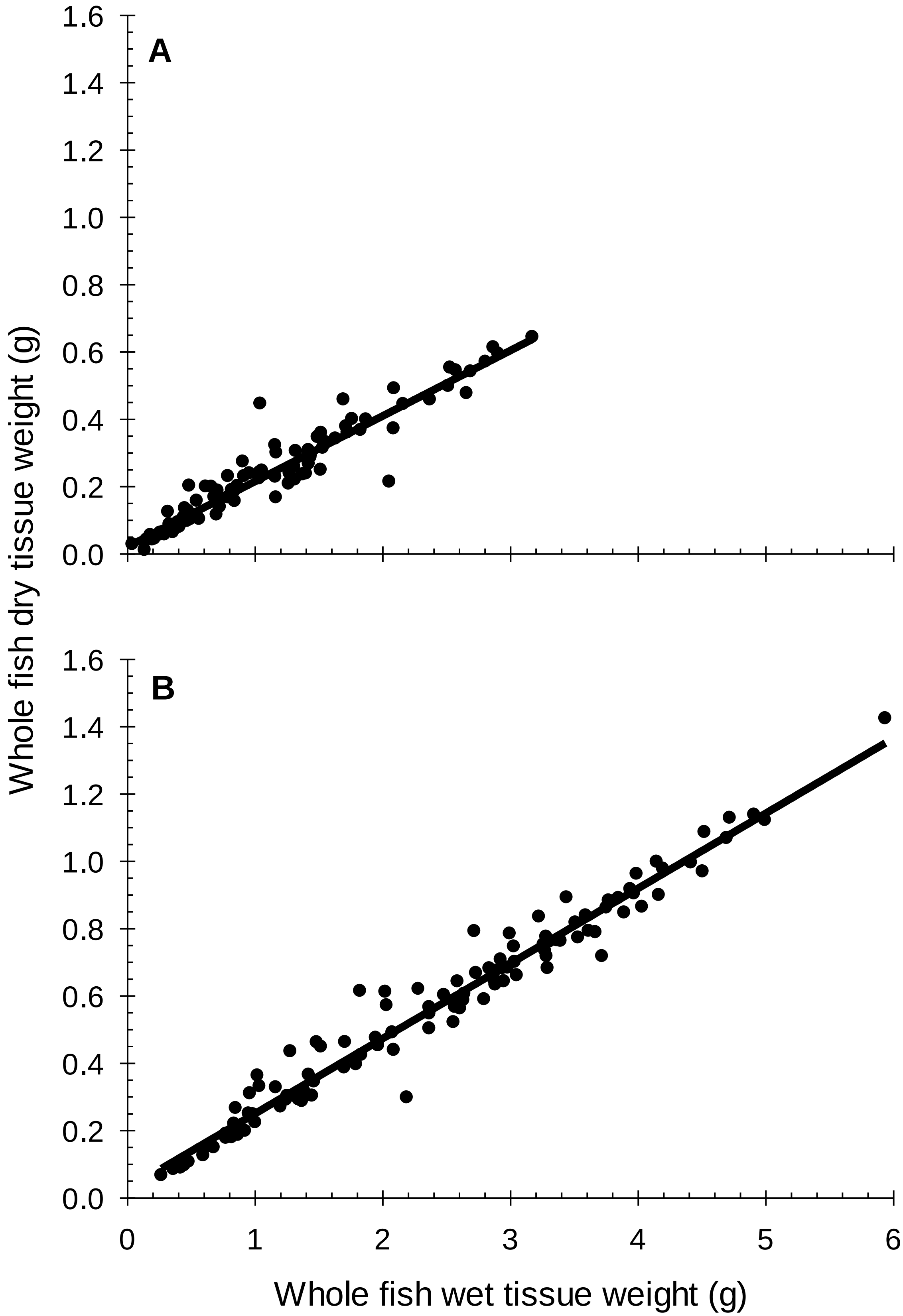

A
B
Whole fish dry tissue weight (g)
Whole fish wet tissue weight (g)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
0
1
2
3
4
5
6

Figure 15: Percent loss (%) from (A) whole fish, (B) somatic, and (C) gonadal wet tissue weight (g) to dry tissue weight (g) for male striped blennies (n = 70). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period from January 2012 (CumWOY 0) through December 2013 (CumWOY 100). Weeks of the spawning season (WOS) are indicated by the inset axes.

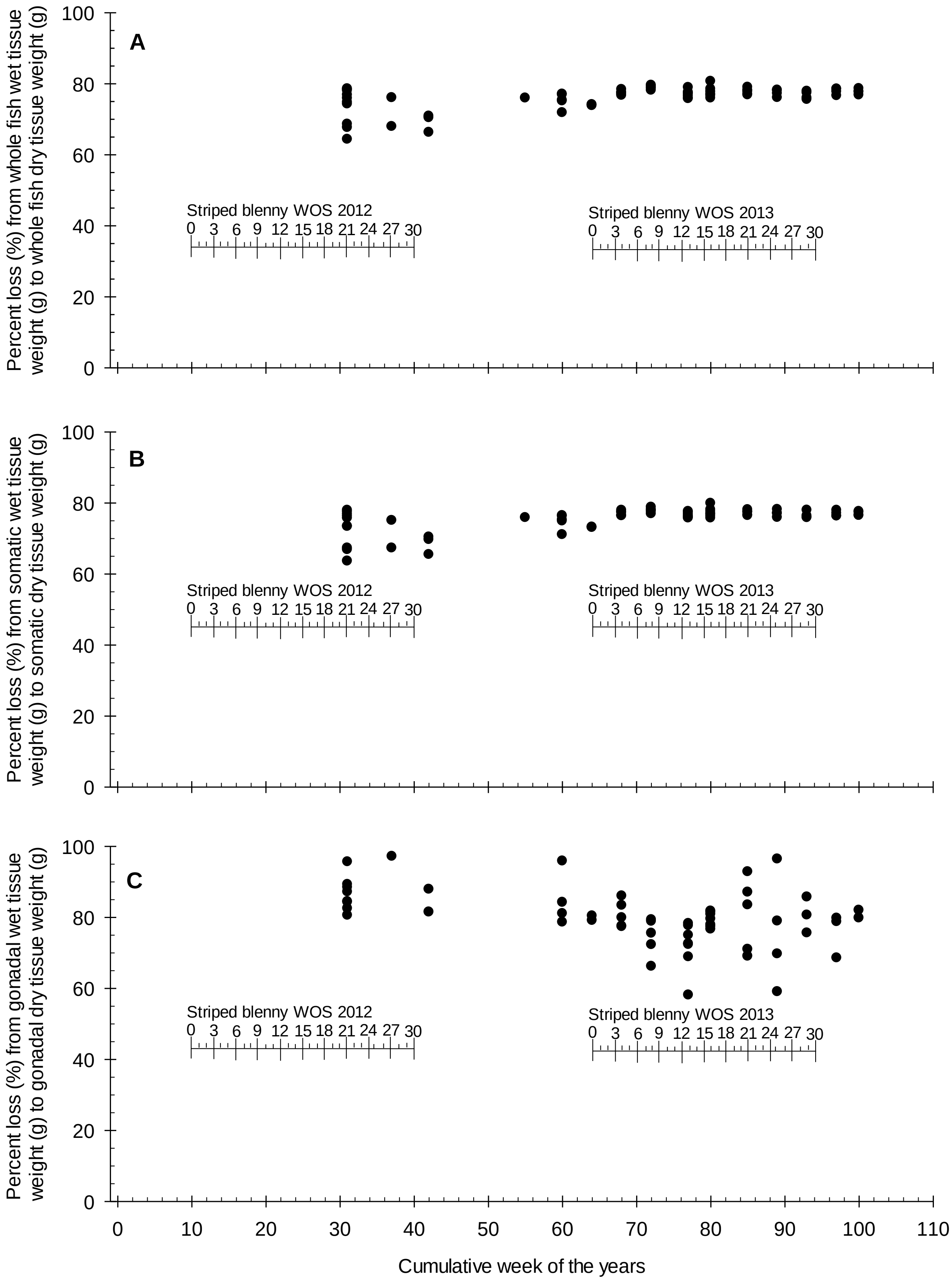

A
B
C
Percent loss (%) from whole fish wet tissue weight (g) to whole fish dry tissue weight (g)
Percent loss (%) from somatic wet tissue weight (g) to somatic dry tissue weight (g)
Percent loss (%) from gonadal wet tissue weight (g) to gonadal dry tissue weight (g)
Striped blenny WOS 2012
Striped blenny WOS 2013
Cumulative week of the years

Figure 16: Percent loss (%) from (A) whole fish, (B) somatic, and (C) gonadal wet tissue weight (g) to dry tissue weight (g) for female striped blennies (n = 42). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period from January 2012 (CumWOY 0) through December 2013 (CumWOY 100). Weeks of the spawning season (WOS) are indicated by the inset axes.

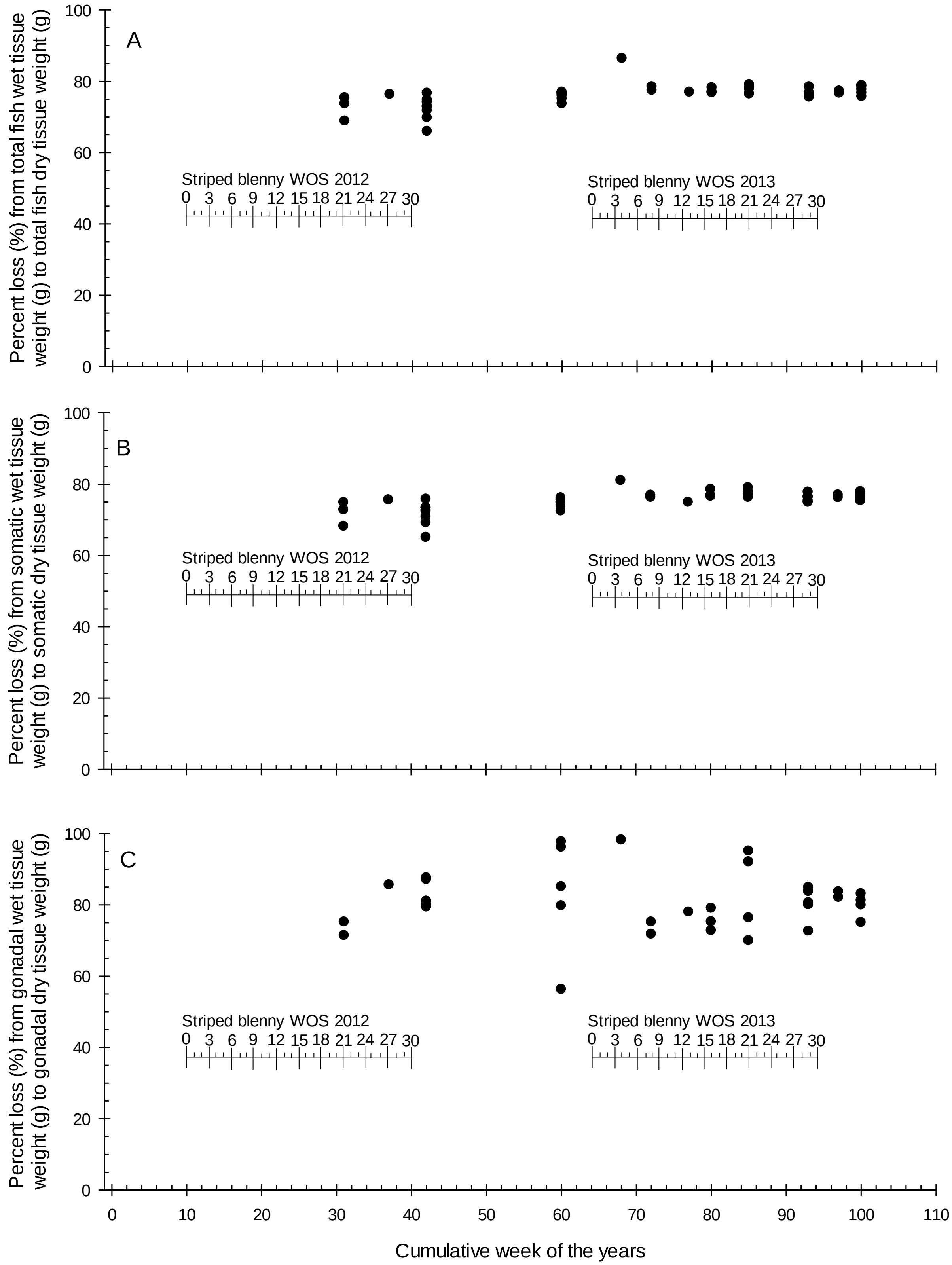

A
B
C
Percent loss (%) from total fish wet tissue weight (g) to total fish dry tissue weight (g)
Percent loss (%) from somatic wet tissue weight (g) to somatic dry tissue weight (g)
Percent loss (%) from gonadal wet tissue weight (g) to gonadal dry tissue weight (g)
Striped blenny WOS 2012
Striped blenny WOS 2013
Cumulative week of the years

Figure 17: The relationship between standard length (mm) and whole fish wet tissue weight (g) for naked goby males (A, n = 85, R^2 = 0.81, SL range 20-55 mm) and females (B, n = 14, R^2 = 0.67, SL range 26-44 mm), and for striped blenny males (C, n = 70, R^2 = 0.88, SL range 26-66 mm) and females (D, n = 42, R^2 = 0.88, SL range 26-56 mm). Coefficients for the fitted power curves are presented in Table 5.

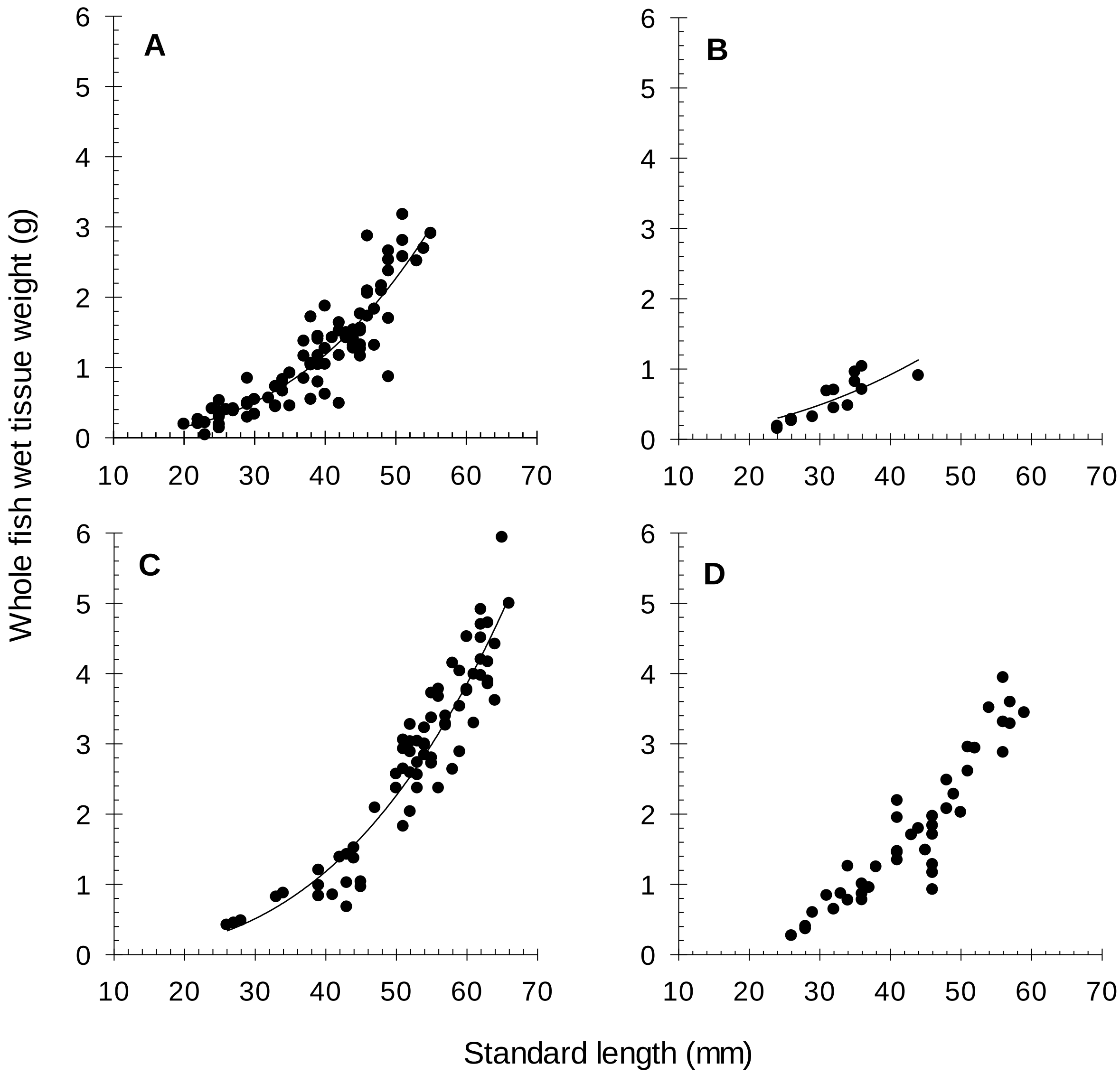
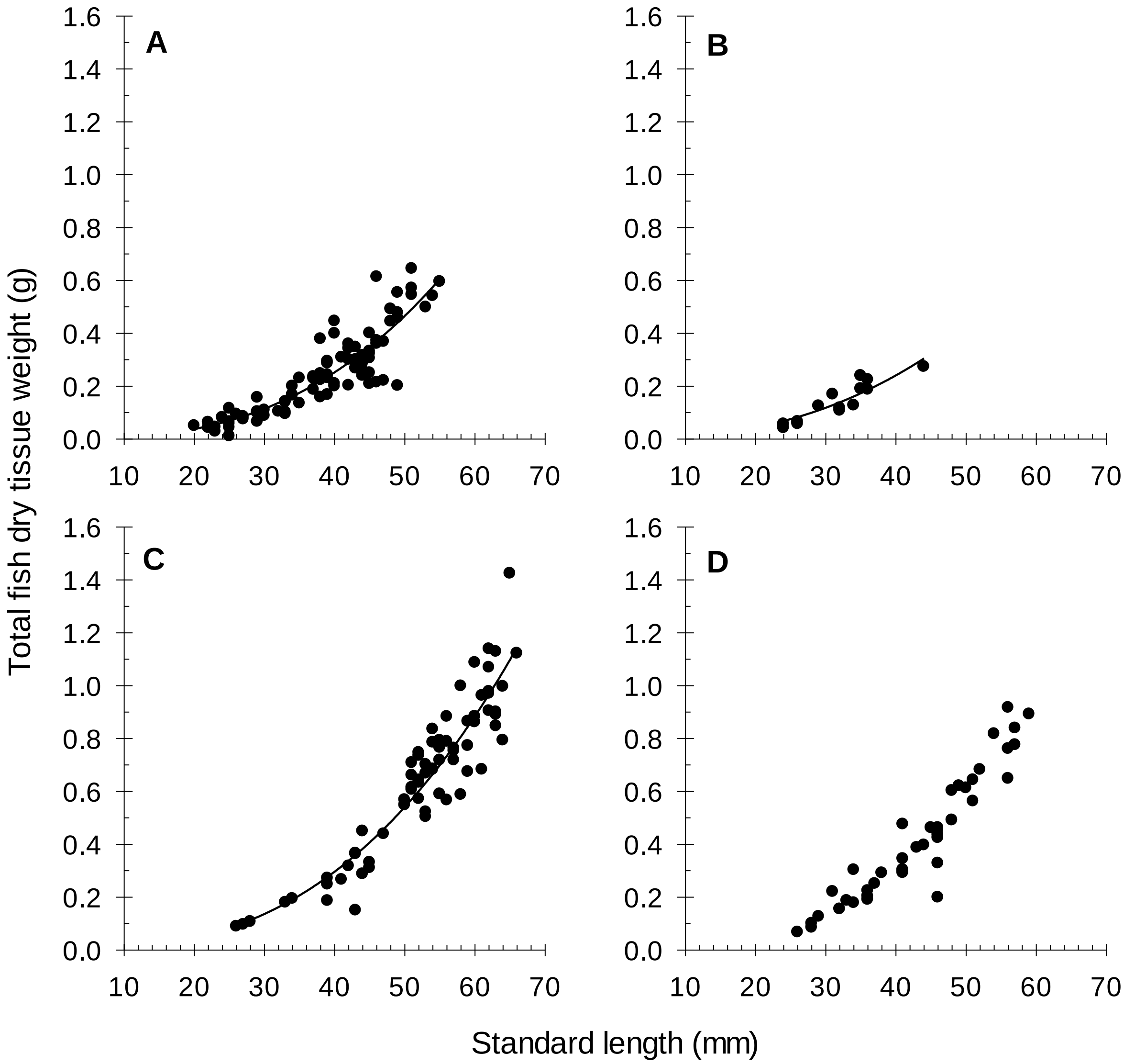

A
B
C
D
Whole fish wet tissue weight (g)
Standard length (mm)
0
1
2
3
4
5
6
10
20
30
40
50
60
70

Figure 18: The relationship between standard length (mm) and whole fish dry tissue weight (g) for naked goby males (A, n = 85, R^2 = 0.80) and females (B, n = 14, R^2 = 0.81), and for striped blenny males (C, n = 70, R^2 = 0.85) and females (D, n = 42, R^2 = 0.91). C, n = 70, R^2 = 0.85) and females (D, n = 42, R^2 = 0.91). Coefficients for the fitted power curves are presented in Table 5.



A
B
C
D
Total fish dry tissue weight (g)
Standard length (mm)

Male naked goby and striped blenny weight increased at approximately the same rate (b = 2.93, goby; b = 2.92, blenny) relative to standard length (Table 5; Figure 17A and 17C). Female naked goby weight increased at a slower rate (b = 2.19) than female striped blenny weight (b = 2.76) relative to standard length (Table 6). The different rates observed between naked goby and striped blenny females are likely due to the absence of naked goby females > 45 mm SL.

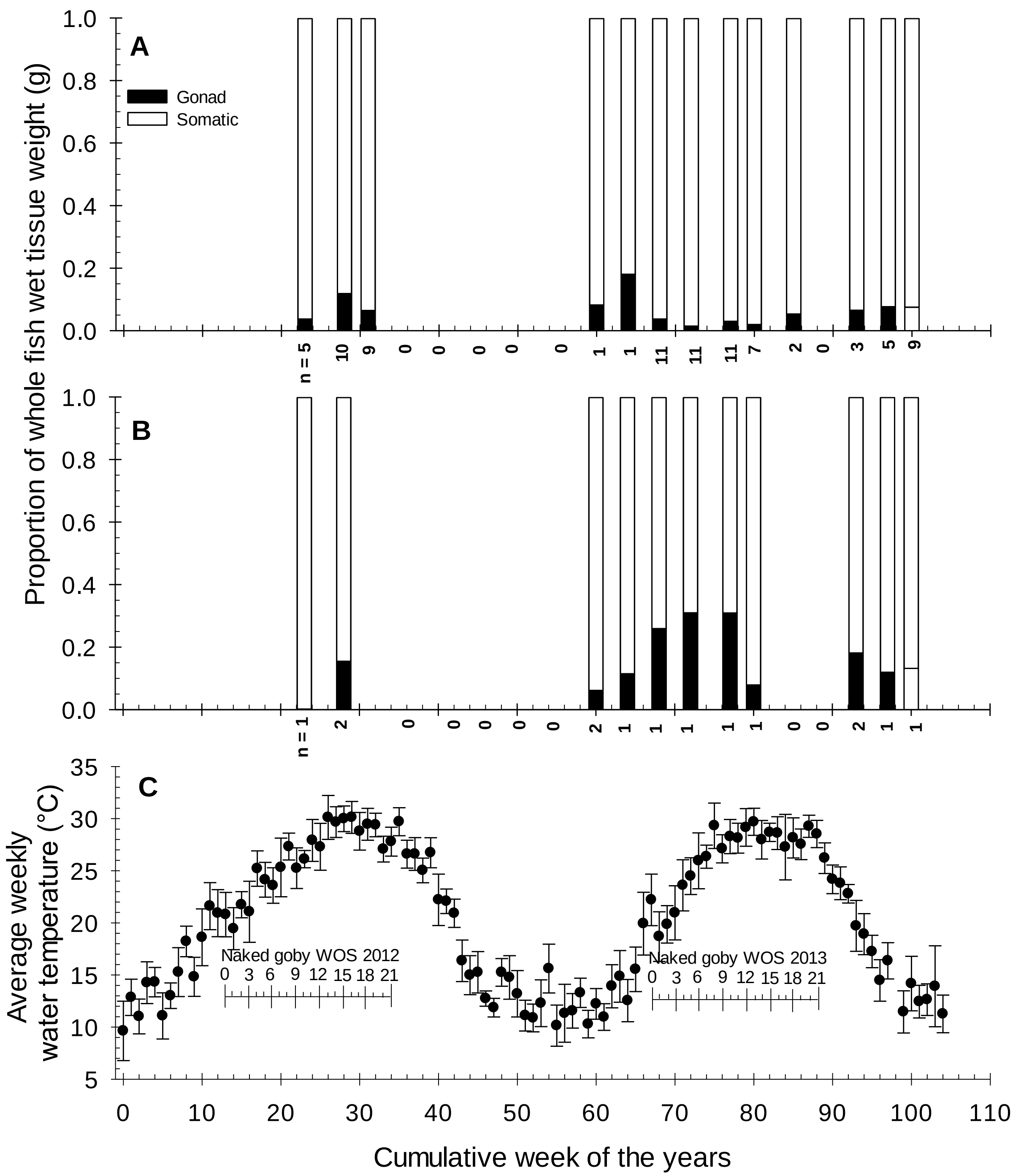
Gonadosomatic indices. The proportion of male naked goby gonad tissue relative to somatic tissue ranged from 0.01 to 0.20 (Figure 19A). Increases in the proportion of goby male gonad tissue and GSI values occurred during week 15 of the 2012 spawning season (WT = 30°C, CumD = 2047) and week 0 of the 2013 spawning season (WT = 22°C, CumD = 328). Male naked goby GSI values ranged from 0% to 8% (Figure 20A). The weeks that male naked goby GSI values were the highest corresponded to weeks when the most naked goby nests were observed (Figure 4A). There were no significant relationships between male naked goby GSI values and water temperature, day-length, or CumD (Pearson correlation; Table 6).

The proportion of naked goby female gonad tissue relative to somatic tissue ranged from 0.05 to 0.40 (Figure 19B). Increases in the proportion of goby female gonad tissue and GSI values began 3 weeks prior to the 2013 spawning season (WT = 13°C; CumD = 110), and reached maximum values between weeks 5-10 of the 2013 spawning season (WT = 28-30°C; CumD = 630-1300; Figure 19B). Female GSI values ranged from 0% to 28% (Figure 20B). Female naked goby GSI values were significantly and positively correlated with day-length, but not significantly correlated with water temperature or

Table 6: Pearson correlation coefficients (r) with (standard error) used to describe the relationships between male and female GSI values and cumulative day-degrees, average weekly day-length (hr), and average weekly water temperature (°C) for naked gobies and striped blennies. Asterisks indicate significance at the alpha = 0.05 level. n equals the number of fish measured.

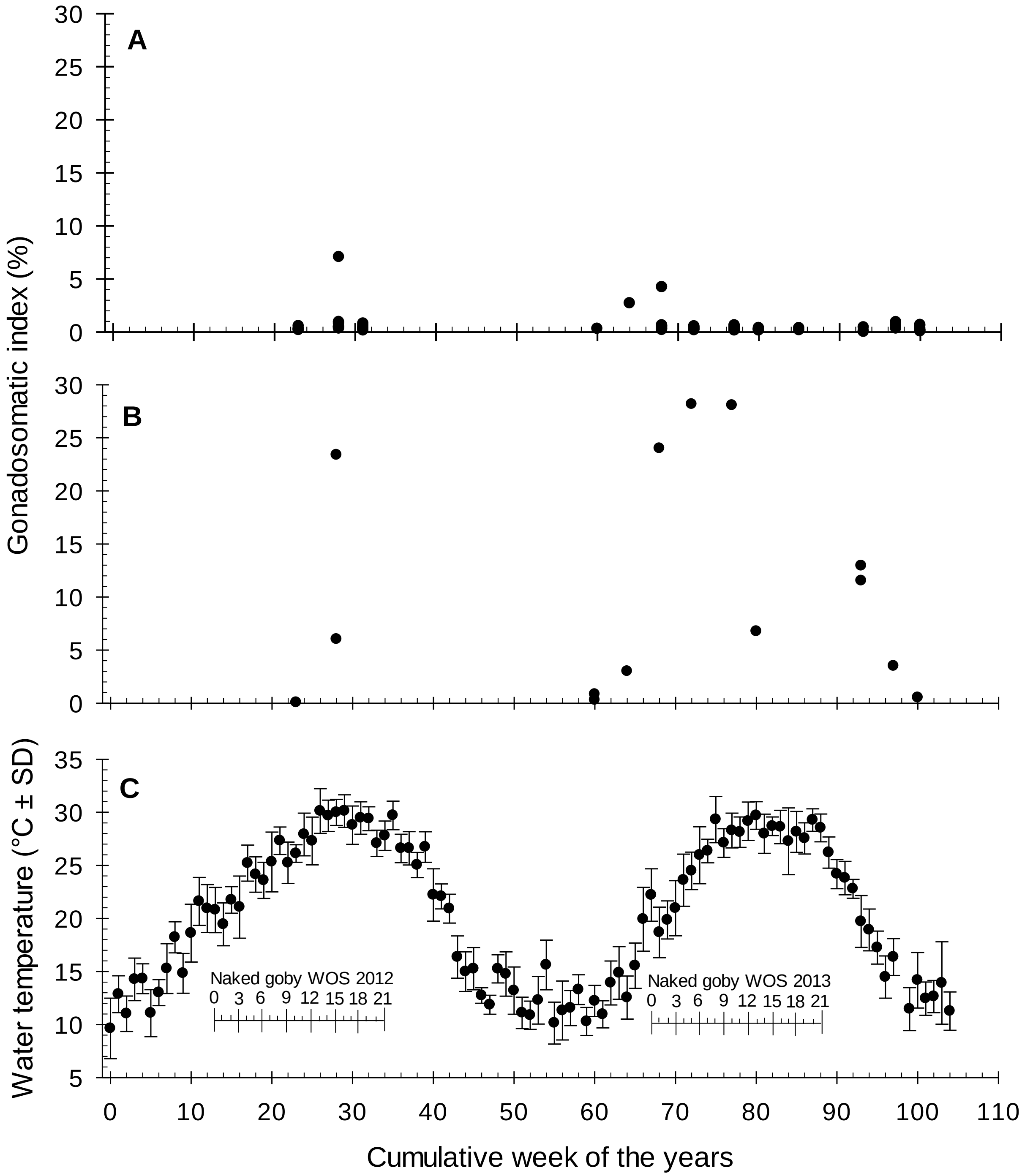
Species	Sex	Variables	n	r	p-value
Naked goby	Male	GSI: Cumulative day-degrees	68	-0.02	0.88
		GSI: Day-length (hr)	85	0.02	0.80
		GSI: Water temperature (°C)	85	-0.01	0.90
	Female	GSI: Cumulative day-degrees	10	0.23	0.53
		GSI: Day-length (hr)	14	0.53	<0.05*
		GSI: Water temperature (°C)	14	0.49	0.07
Striped blenny	Male	GSI: Cumulative day-degrees	59	-0.44	<0.05*
		GSI: Day-length (hr)	70	-0.02	0.89
		GSI: Water temperature (°C)	70	-0.25	<0.05*
	Female	GSI: Cumulative day-degrees	27	0.03	0.89
		GSI: Day-length (hr)	42	0.67	<0.05*
		GSI: Water temperature (°C)	42	0.44	<0.05*

Figure 19: The proportion of gonad wet tissue weight (g) and somatic wet tissue weight (g) for male (A, n = 85) and female (B, n = 14) naked goby adults, and (C) average weekly water temperature (°C ± standard deviation) observed in Crabhaul Creek, North Inlet, SC from January 2012 (CumWOY 0) through December 2013 (CumWOY 100). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period. Weeks of the spawning season (WOS) are indicated by the inset axes. n equals the number of fish measured.



A
B
C
Gonad
Somatic
Proportion of whole fish wet tissue weight (g)
Average weekly water temperature (°C)
Naked goby WOS 2012
Naked goby WOS 2013
Cumulative week of the years

Figure 20: Gonadosomatic index (%) values for male (A, n = 85) and female (B, n = 14) naked goby adults, and (C) average weekly water temperature (°C ± standard deviation) observed in Crabhaul Creek, North Inlet, SC from January 2012 (CumWOY 0) through December 2013 (CumWOY 100). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period. Weeks of the spawning season (WOS) are indicated by the inset axes.



A
B
C
Gonadosomatic index (%)
Water temperature (°C ± SD)
Naked goby WOS 2012
0 3 6 9 12 15 18 21
Naked goby WOS 2013
0 3 6 9 12 15 18 21
Cumulative week of the years

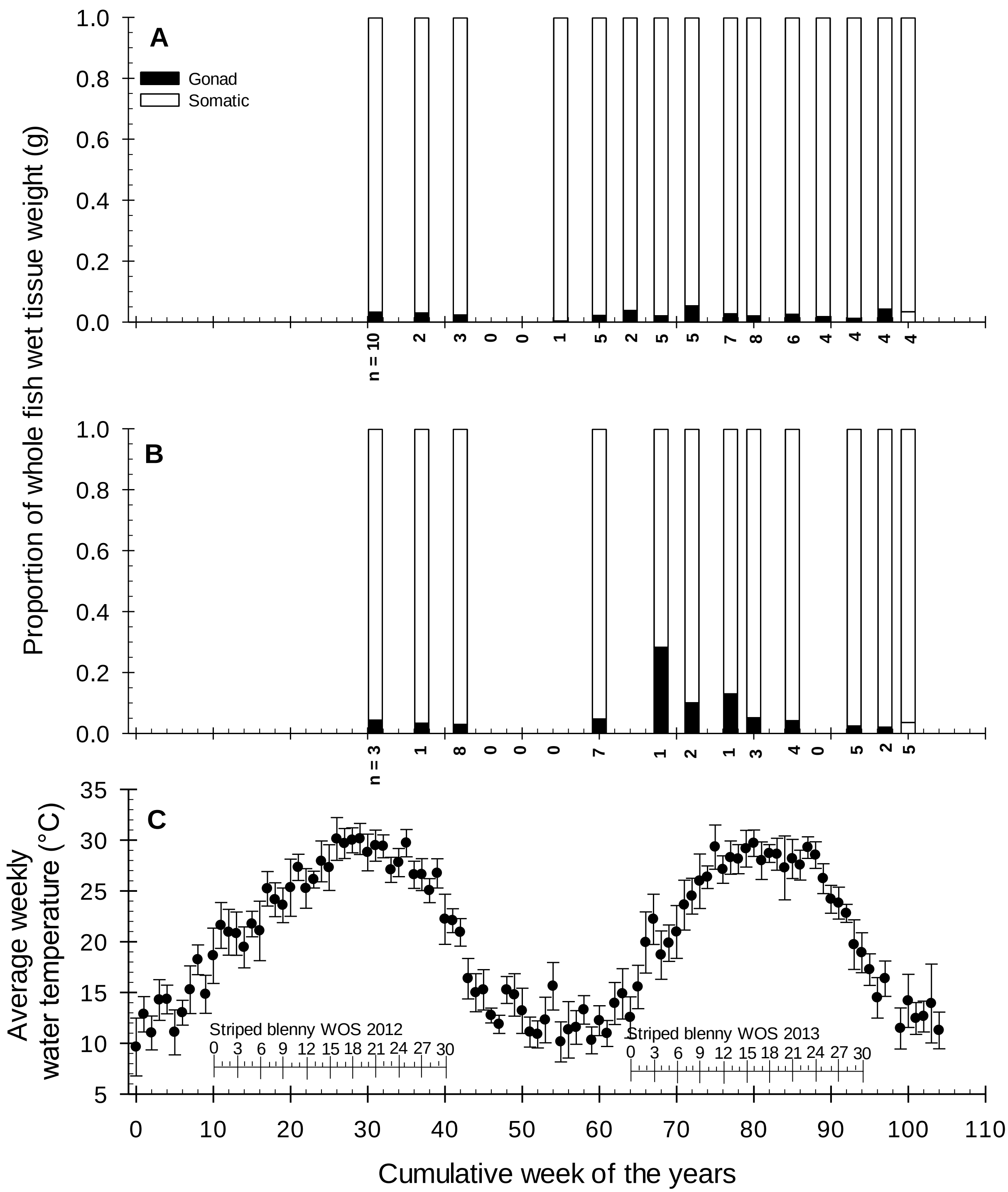
cumulative day-degrees (Pearson correlation; Table 6). Female goby GSI values increased with increasing day-length.

The proportion of male striped blenny gonad tissue relative to somatic tissue ranged from 0.01 to 0.05 (Figure 21A). Increases in male GSI values were observed 3 weeks prior to the start of the 2013 spawning season (WT = 13°C; CumD = 193). Male striped blenny GSI values range from 0% to 2% (Figure 22A). Male striped blenny GSI values were significantly and negatively correlated with water temperature and cumulative day-degrees, but not significantly correlated with day-length (Pearson correlation; Table 6). Male blenny GSI values decreased with increasing water temperature.

The proportion of female striped blenny gonadal tissue relative to somatic tissue ranged from 0.03 to 0.30 (Figure 21B). Female GSI values ranged from 0% to 6% (Figure 22B). Maximum GSI values were observed between weeks 6-9 of the 2013 spawning season when water temperatures were increasing from 25°C to 29°C (CumD = 540-935). Female striped blenny GSI values were significantly and positively correlated with water temperature and day-length, but were not significantly correlated with cumulative day-degrees (Pearson correlation; Table 6). Female blenny GSI values increased with increasing water temperature and day-length.

Female reproductive condition indices. Naked goby FRC ranged from 0.05 to 0.25 (Figure 23). Increases in goby FRC occurred from 3 weeks prior to the 2013 season to week 10 of the 2013 spawning season when increases in female GSI values were also observed (Figure 20B; Figure 23). Maximum FRC values occurred at week 9 of the 2013 spawning season (WT = 30°C; CumD = 1185). Increases in goby FRC corresponded to

Figure 21: The proportion of gonad wet tissue weight (g) and somatic wet tissue weight (g) for male (A, n = 70) and female (B, n = 42) striped blenny adults, and (C) average weekly water temperature (°C ± standard deviation) observed in Crabhaul Creek, North Inlet, SC from January 2012 (CumWOY 0) through December 2013 (CumWOY 100). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period. Weeks of the spawning season (WOS) are indicated by the inset axes. n equals the number of fish measured.



A
Gonad
Somatic
B
C
Proportion of whole fish wet tissue weight (g)
Average weekly water temperature (°C)
n = 10 2 3 0 0 1 5 2 5 5 7 8 6 4 4 4 4
n = 3 1 8 0 0 0 7 1 2 1 3 4 0 5 2 5
Striped blenny WOS 2012
Striped blenny WOS 2013
Cumulative week of the years

Figure 22: Gonadosomatic index (%) values for male (A, n = 70) and female (B, n = 42) striped blenny adults, and (C) average weekly water temperature (°C ± standard deviation) observed in Crabhaul Creek, North Inlet, SC from January 2012 (CumWOY 0) through December 2013 (CumWOY 100). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period. Weeks of the spawning season (WOS) are indicated by the inset axes. n equals the number of fish measured.

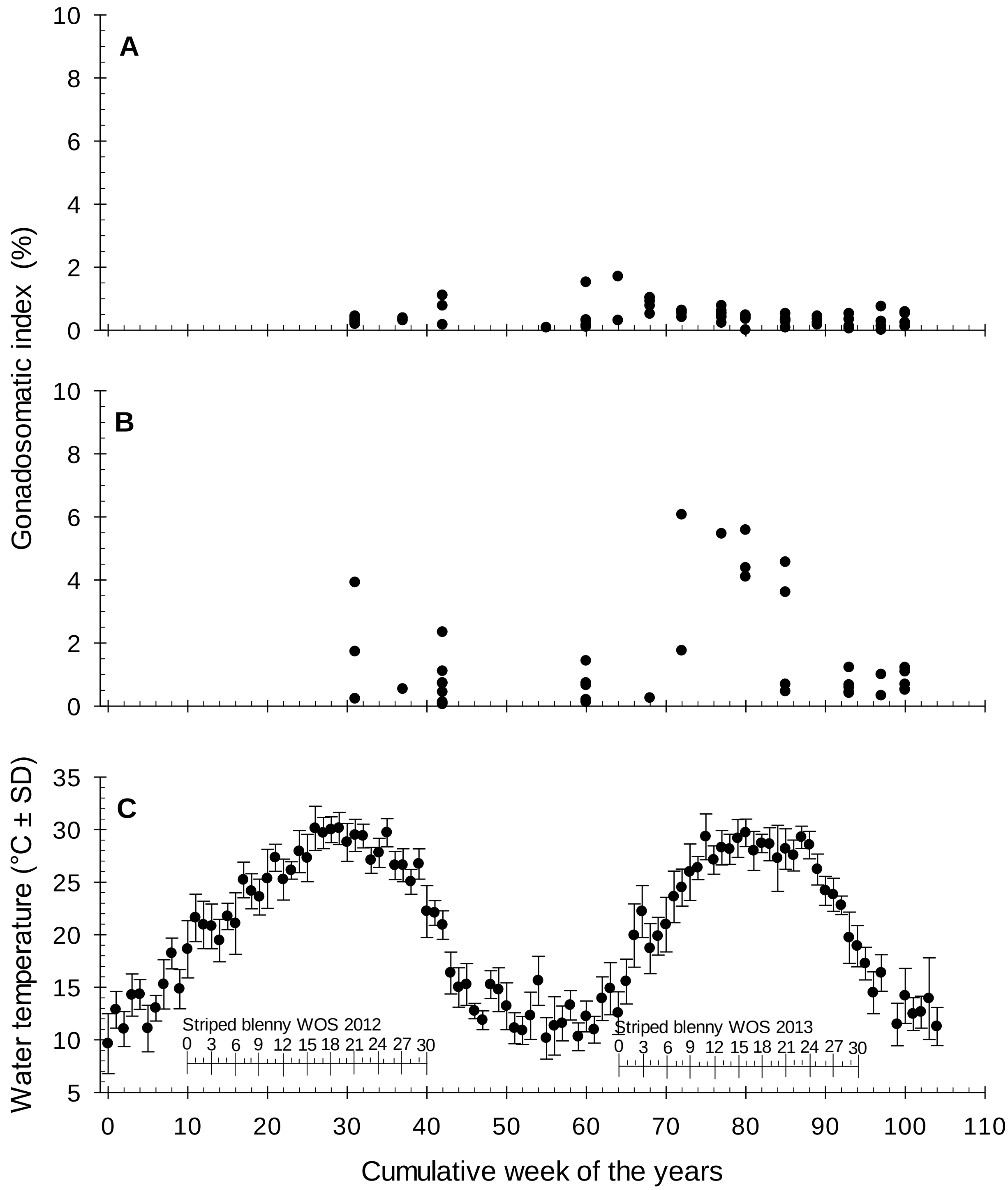
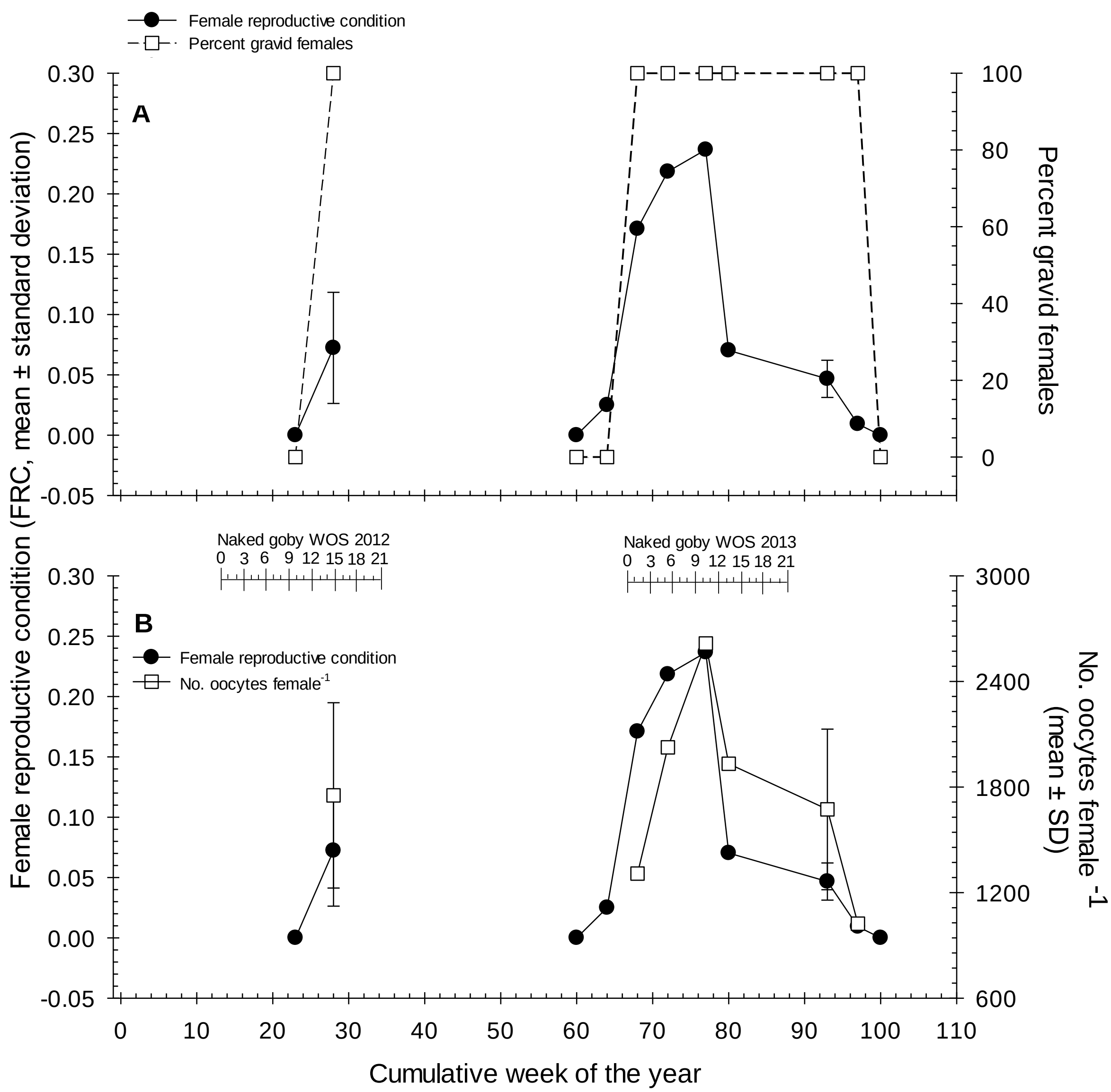

A
B
C
Gonadosomatic index (%)
Water temperature (°C ± SD)
Striped blenny WOS 2012
Striped blenny WOS 2013
Cumulative week of the years

Figure 23: Mean naked goby female reproductive condition (FRC) and the percentage of gravid females (A, n = 14), and mean naked goby female reproductive condition and the mean number (No.) of oocytes female^{-1} measured for gravid females (B, n = 9). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period from January 2012 (CumWOY 0) through December 2013 (CumWOY 100). Weeks of the spawning season (WOS) are indicated by the inset axes. n equals the number of fish measured.



Female reproductive condition
Percent gravid females
A
B
Female reproductive condition
No. oocytes female-1
Naked goby WOS 2012
Naked goby WOS 2013
0 3 6 9 12 15 18 21
Female reproductive condition (FRC, mean ± standard deviation)
Percent gravid females
No. oocytes female -1 (mean ± SD)
Cumulative week of the year

increases in the percentage of gravid females (Figure 23A) and the number of oocytes female^{-1} (Figure 23B). Reductions in FRC and the number of oocytes female^{-1} were observed 3 weeks after the maximum was reached and declined through November 2013.

Striped blenny FRC was lower than naked goby FRC, and ranged from 0.0 to 0.07 (Figure 24). When standardized by length, striped blenny females invested approximately four times less into gonadal tissue development than naked goby females. Increases in blenny FRC were observed from week 6-15 of the 2013 spawning season when increases in female blenny GSI values were observed (Figure 22B; Figure 24). Maximum FRC values occurred during week 15 of the 2013 spawning season (WT = 30°C; CumD = 1600). Increases in blenny FRC corresponded to increases in the percentage of gravid females (Figure 24A) and the number of oocytes female^{-1} (Figure 24B). Reductions in FRC and number of oocytes female^{-1} were observed 5 weeks after the maximum was reached and continued through December 2013.

Oocyte diameter. The number of oocytes estimated from gravid naked goby females (n = 9) ranged between 1,024 and 2,616 for females between 29 mm and 36 mm SL. Naked goby oocyte diameters ranged between 0.42 mm and 0.78 mm (Figure 25A) . Oocyte diameters varied less than 0.15 mm within individual females. Oocyte diameters were not significantly affected by lobe section (anterior, middle, and posterior), lobe (right and left), or the interaction between section and lobe within an individual female (ANOVA, Table 7). Naked goby females collected during weeks 13-15 of the spawning season (n = 3, 29-36 mm SL) had oocyte diameters approximately 0.30 mm smaller than females collected before week 10 of the spawning season (n =3, 31-36 mm SL; Figure 25A). When oocyte diameters were standardized by female standard length, oocyte diameters

Table 7: Summary of two-way ANOVAs performed on oocyte diameters (mm) measured from the anterior, middle, and posterior sections of both the right and left ovarian lobes for individual female naked gobies and striped blennies. WOS indicates week of the spawning season. Asterisks indicate significance at alpha = 0.05.

Species	Fish #	WOS	Factor	df	F	p-value
Naked goby	1	1	Lobe	1	1.44	0.24
			Section	2	0.38	0.67
			Lobe*Section	2	0.14	0.87
	2	5	Lobe	1	1.38	0.25
			Section	2	0.43	0.66
			Lobe*Section	2	0.26	0.78
	3	10	Lobe	1	2.35	0.13
			Section	2	2.02	0.14
			Lobe*Section	2	2.34	0.79
	4	13	Lobe	1	0.02	0.88
			Section	2	0.07	0.94
			Lobe*Section	2	0.02	0.98
	5	15	Lobe	1	0.58	0.45
			Section	2	0.07	0.93
			Lobe*Section	2	0.16	0.85
	6	15	Lobe	1	0.33	0.57
			Section	2	0.02	0.98
			Lobe*Section	2	0.30	0.74
Striped blenny	1	8	Lobe	1	0.22	0.64
			Section	2	2.24	0.12
			Lobe*Section	2	0.22	0.81
	2	13	Lobe	1	1.22	0.28
			Section	2	0.74	0.48
			Lobe*Section	2	2.53	0.09
	3	16	Lobe	1	0.12	0.73
			Section	2	0.12	0.88
			Lobe*Section	2	0.04	0.96
	4	16	Lobe	1	0.72	0.34
			Section	2	0.12	0.89
			Lobe*Section	2	0.46	0.63
	5	16	Lobe	1	0.01	0.93
			Section	2	0.04	0.96
			Lobe*Section	2	0.17	0.85
	6	21	Lobe	1	0.87	0.35
			Section	2	0.10	0.91
			Lobe*Section	2	0.01	1.00

Figure 24: Mean striped blenny female reproductive condition (FRC) and the percentage of gravid females (A, n = 42), and mean female reproductive condition and the mean number (No.) of oocytes female^{-1} measured for gravid females (B, n = 6). Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period from January 2012 (CumWOY 0) through December 2013 (CumWOY 100). Weeks of the spawning season (WOS) are indicated by the inset axes. n equals the number of fish measured.

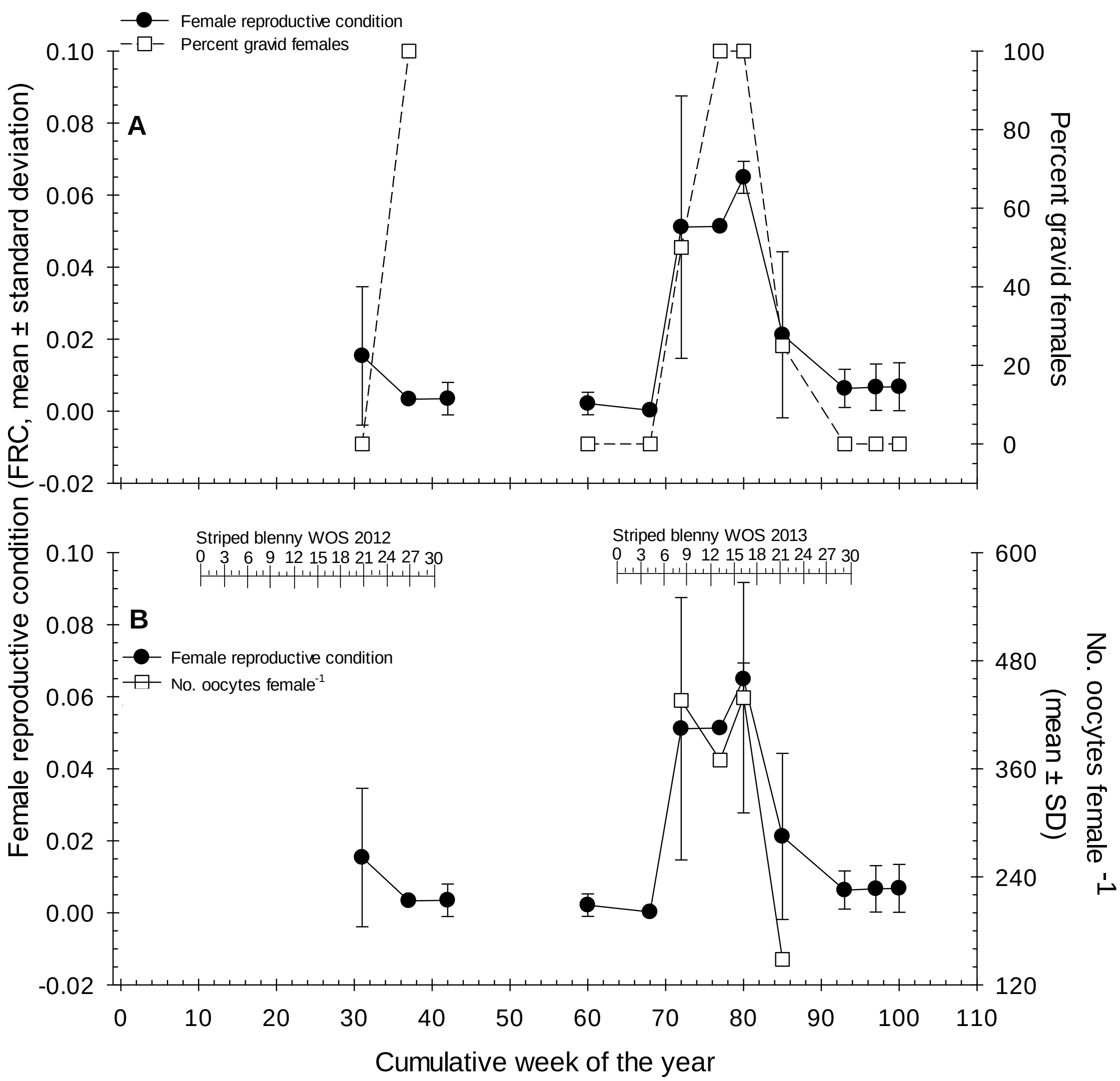
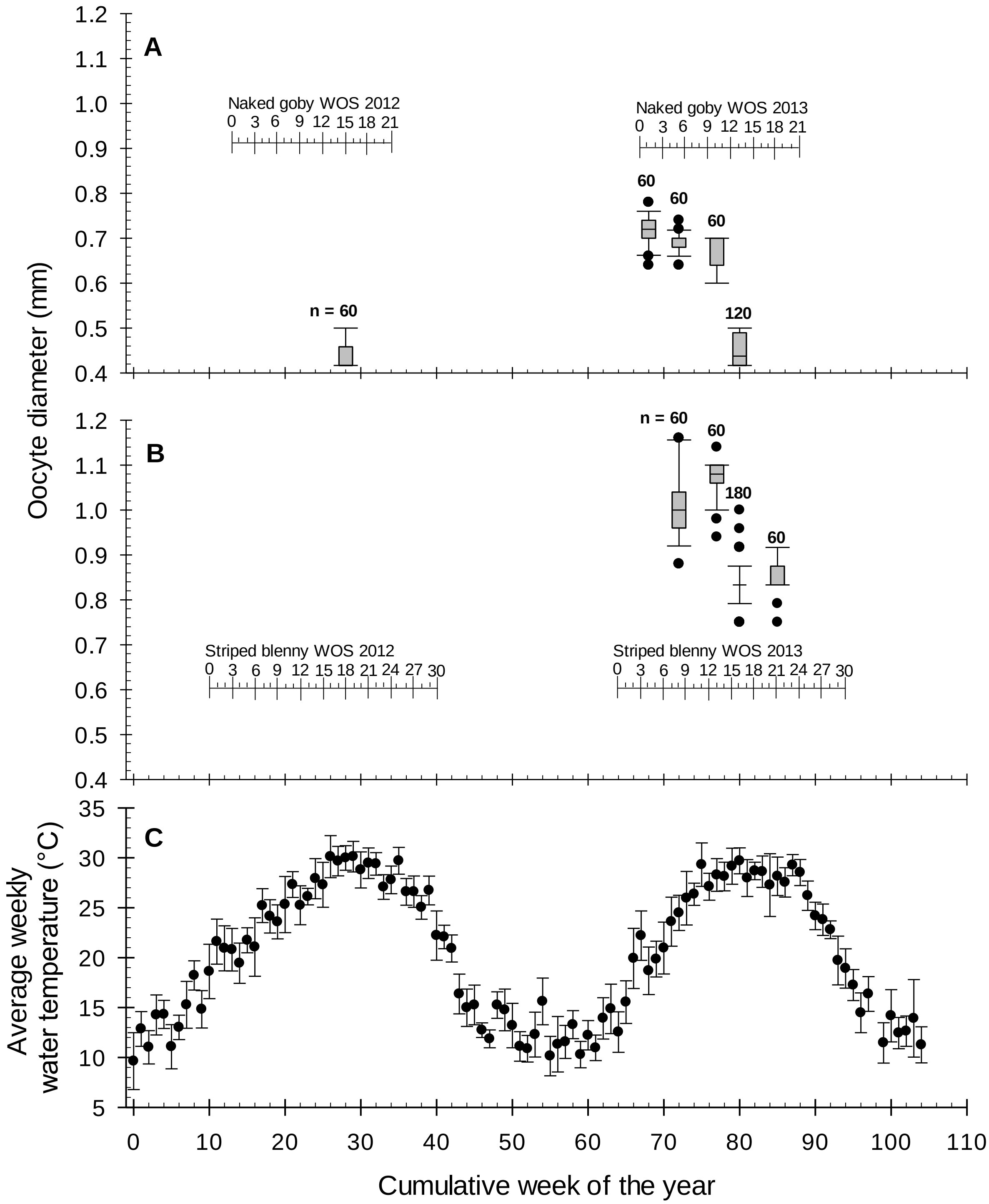

Female reproductive condition
Percent gravid females
A
B
Female reproductive condition (FRC, mean ± standard deviation)
Percent gravid females
Striped blenny WOS 2012
Striped blenny WOS 2013
Female reproductive condition
No. oocytes female-1
No. oocytes female -1 (mean ± SD)
Cumulative week of the year

Figure 25: Oocyte diameter (mm) measured for 6 naked goby (A) and 6 striped blenny (B) females by collection week and (C) average weekly water temperature (°C ± standard deviation) observed in Crabhaul Creek, North Inlet, SC from January 2012 (CumWOY 0) through December 2013 (CumWOY 100). Weeks of the spawning (WOS) are indicated by the inset axes. Sixty oocytes were measured from each female. n equals the number of oocytes measured for each box whisker plot.


A
B
C
Naked goby WOS 2012
Naked goby WOS 2013
Striped blenny WOS 2012
Striped blenny WOS 2013
n = 60
60
120
180
Oocyte diameter (mm)
Average weekly water temperature (°C)
Cumulative week of the year

measured before week 10 of the spawning season were 30% larger than oocyte diameters measured between weeks 13 and 15 of the spawning season (Figure 26A).

The number of oocytes observed within gravid striped blenny females (n = 6) ranged between 148 and 585 oocytes for females ranging between 44 and 56 mm SL. Striped blenny oocyte diameters ranged between 0.75 mm and 1.16 mm (Figure 25B). Oocyte diameters varied less than 0.20 mm within individual females. Oocyte diameters were not significantly affected by lobe section (anterior, middle, and posterior), lobe (right and left), or the interaction between section and lobe within an individual female (ANOVA, Table 7). Striped blenny females collected between weeks 8 and 13 of the spawning season (n = 2, 46-51 mm SL) had oocyte diameters approximately 0.20 mm larger than females collected between weeks 16 and 21 of the spawning season (n = 4, 44-56 mm SL; Figure 25B). When standardized by female standard length, oocyte diameters measured before week 15 of the spawning season were 20% larger than oocyte diameters measured after week 15 (Figure 26B).

Female reproductive relationships. Naked goby clutch size (the number of oocytes $female^{-1}$) scaled non-linearly with female SL (R^2 = 0.74; Table 8; Figure 27A) and body depth (R^2 = 0.75; Table 8; Figure 27B), but had no relationship with whole fish WTW (R^2 = 0.58; Table 8; Figure 27C), and gonad WTW (R^2 = 0.34; Table 8; Figure 27D). Female naked goby gonad WTW scaled non-linearly with whole fish WTW (R^2 = 0.72; Table 8; Figure 28E), but had no relationship with SL (R^2 = 0.29; Table 8; Figure 28A) or body depth (R^2 = 0.16; Table 8; Figure 28C). Because females spawn sequentially, they are likely at different stages of gonadal development at different times. Therefore, females of the same length collected at different dates or on the same date may have

Table 8: Power equation coefficients (*a*,*b*) with (standard error) used to describe naked goby and striped blenny female reproductive relationships. Model coefficients and equations are defined in the text. SL equals standard length (mm). BD equals body depth (mm). WTW equals wet tissue weight (g). n equals the number of fish measured.

Species	Relationship	n	*a*		*b*		R^2
Naked goby	SL: No. eggs $female^{-1}$	9	1.62	(2.95)	2.02	(0.52)	0.74
	BD: No. eggs $female^{-1}$	9	44.3	(42.4)	2.17	(0.55)	0.75
	Whole WTW: No. eggs $female^{-1}$	9	$2.22x10^3$	(198)	0.42	(0.15)	0.58
	Gonad WTW: No. eggs $female^{-1}$	9	$2.62x10^3$	(569)	0.16	(0.09)	0.34
	SL: Gonad WTW	9	$2.57x10^{-8}$	$(3.27x10^{-7})$	4.39	(3.59)	0.29
	BD: Gonad WTW	9	$5.64x10^{-4}$	$(3.70x10^{-3})$	3.12	(3.77)	0.16
	Whole WTW: Gonad WTW	9	0.26	(0.04)	2.83	(1.02)	0.72
Striped blenny	SL: No. eggs $female^{-1}$	6	$1.07x10^{-4}$	$5.04x10^{-4})$	3.85	(1.20)	0.75
	BD: No. eggs $female^{-1}$	6	0.03	(0.08)	3.73	(1.16)	0.75
	Whole WTW: No. eggs $female^{-1}$	6	$2.47x10^3$	$(3.14x10^3)$	0.91	(0.64)	0.42
	Gonad WTW: No. eggs $female^{-1}$	6	110	(67.6)	1.29	(0.59)	0.61
	SL: Gonad WTW	6	$1.17x10^{-4}$	$(4.84x10^{-4})$	1.79	(1.06)	0.46
	BD: Gonad WTW	6	$1.48x10^{-3}$	$(3.92x10^{-3})$	1.74	(1.02)	0.46
	Whole WTW: Gonad WTW	6	0.06	(0.02)	0.74	(0.36)	0.56

Figure 26: Average standardized oocyte diameter for female naked gobies (A) and striped blennies (B). Oocyte diameters (mm) were standardized by female standard length (mm). Each point represents sixty standardized oocytes measured from each female. Cumulative week of the years (CumWOY) corresponds to the sampling week within the two year period from January 2012 (CumWOY 0) through December 2013 (CumWOY 100).Weeks of the spawning (WOS) are indicated by the inset axes.

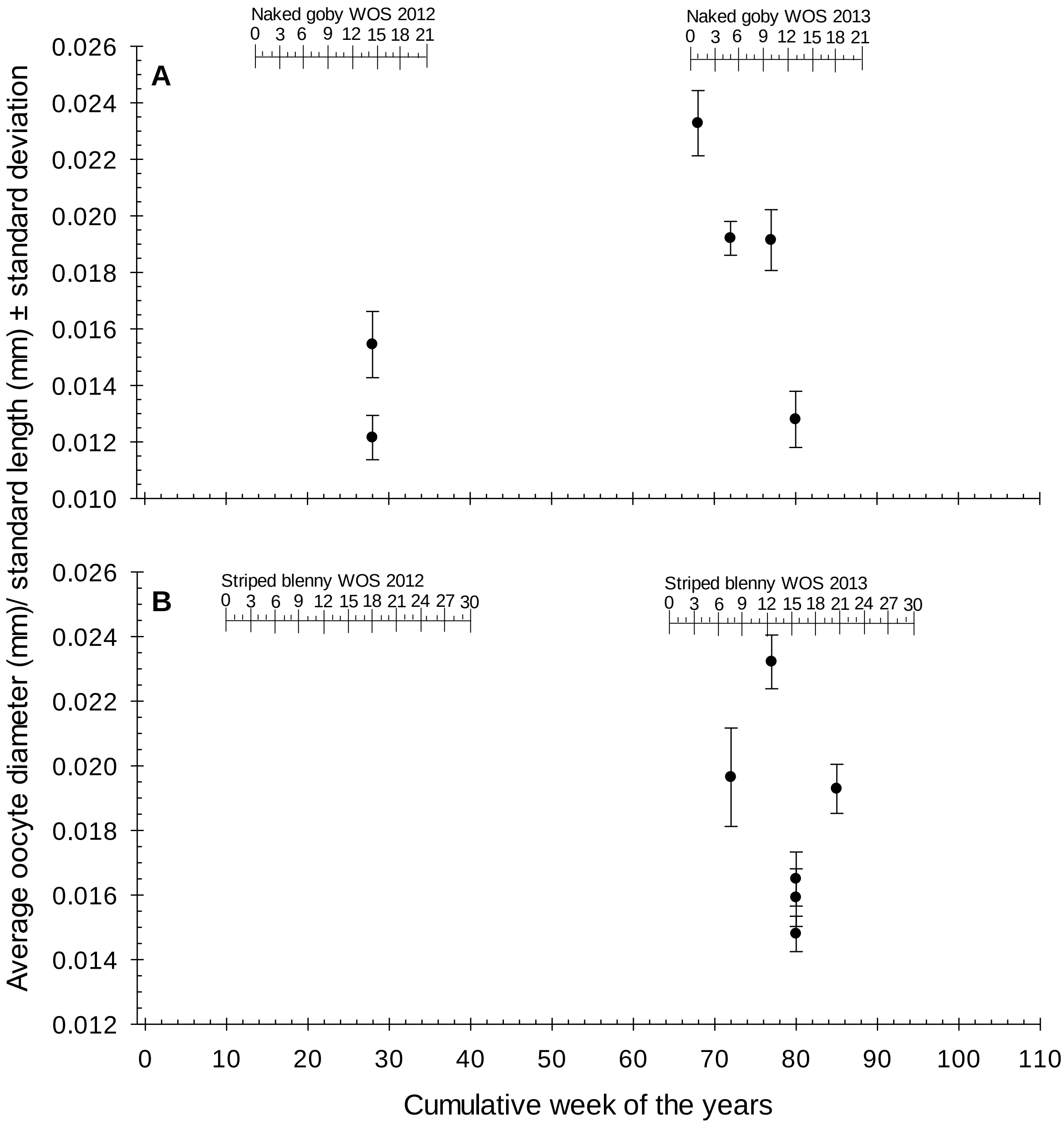

Naked goby WOS 2012
0 3 6 9 12 15 18 21
Naked goby WOS 2013
0 3 6 9 12 15 18 21
A
Striped blenny WOS 2012
0 3 6 9 12 15 18 21 24 27 30
Striped blenny WOS 2013
0 3 6 9 12 15 18 21 24 27 30
B
Average oocyte diameter (mm)/ standard length (mm) ± standard deviation
0.026
0.024
0.022
0.020
0.018
0.016
0.014
0.012
0.010
0 10 20 30 40 50 60 70 80 90 100 110
Cumulative week of the years

Figure 27: The relationship between naked goby (A) standard length (mm), (B) whole fish wet tissue weight (g) and (C) gonad wet tissue weight (g) and number of eggs female^{-1} for 9 females. Model coefficients are presented in Table 8.

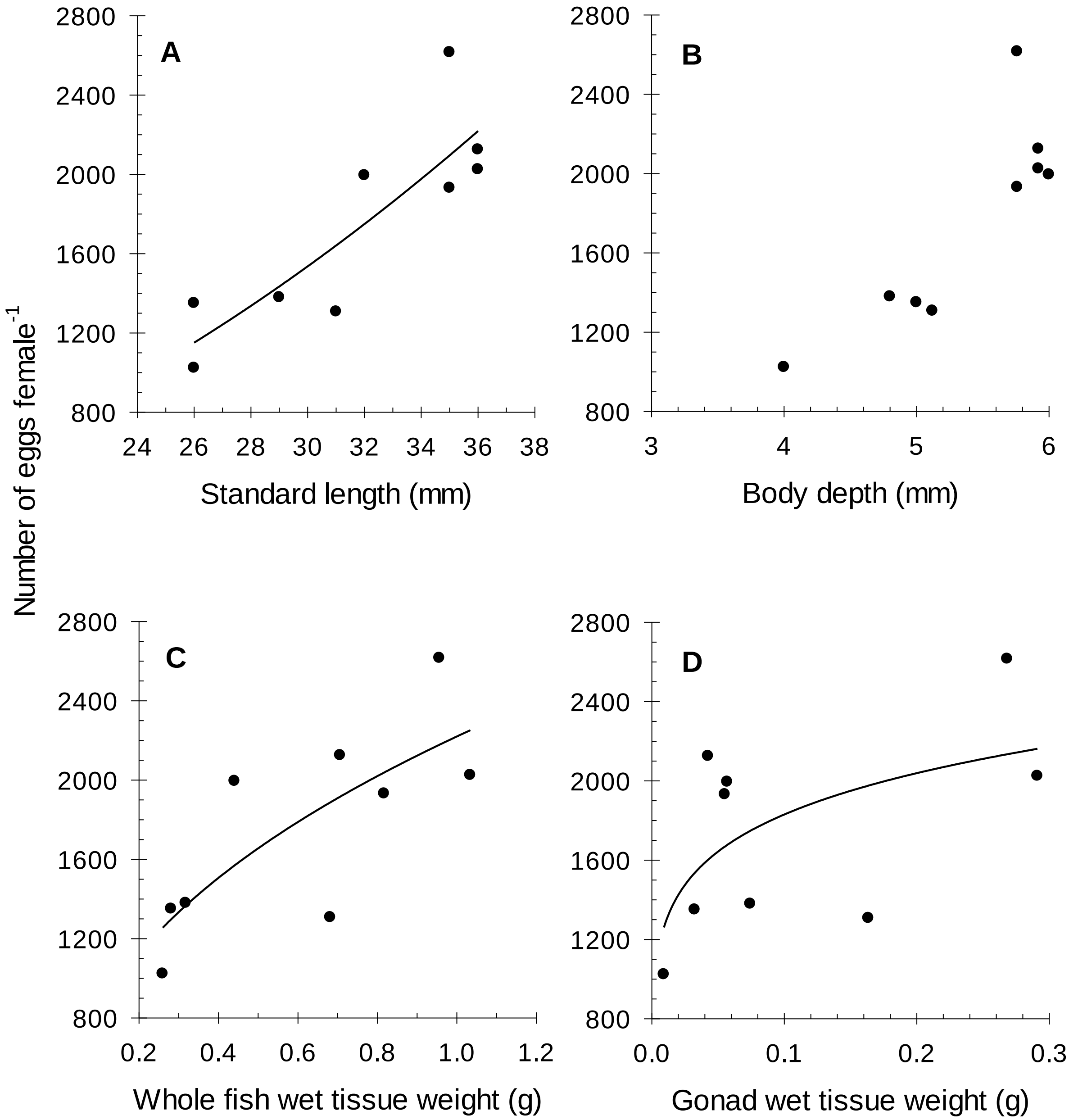
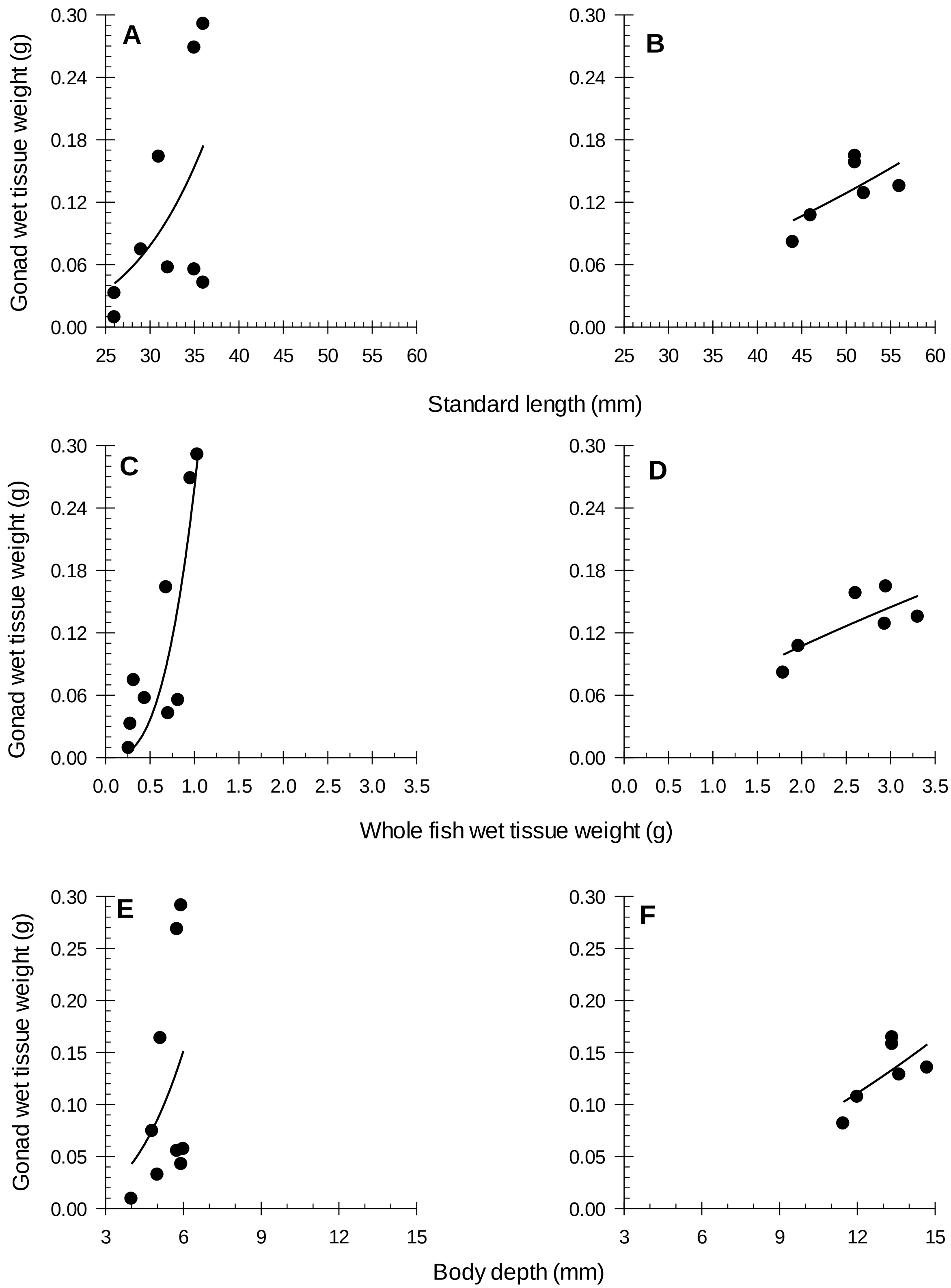

A
B
C
D
Number of eggs female^{-1}
2800
2400
2000
1600
1200
800
24 26 28 30 32 34 36 38
3 4 5 6
0.2 0.4 0.6 0.8 1.0 1.2
0.0 0.1 0.2 0.3
Standard length (mm)
Body depth (mm)
Whole fish wet tissue weight (g)
Gonad wet tissue weight (g)

Figure 28: The relationship between standard length (mm) and gonad wet tissue weight (g) for naked goby females (A, n = 9) and striped blenny females (B, n = 6), and the relationship between whole fish wet tissue weight (g) and gonad wet tissue weight (g) for naked goby females (C, n = 9) and striped blenny females (D, n = 6). Model coefficients are presented in Table 8.

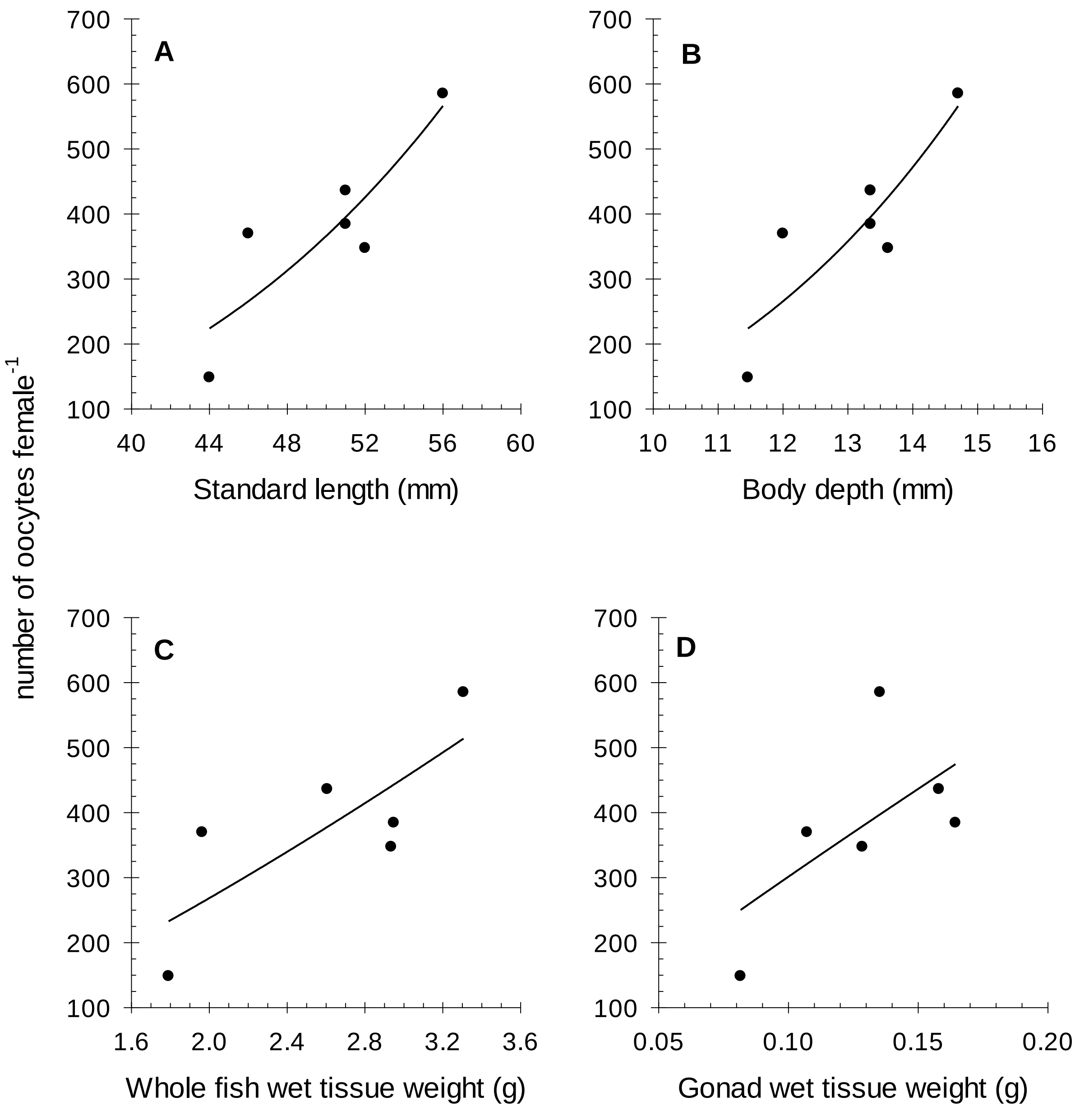


A
B
C
D
E
F
Gonad wet tissue weight (g)
0.00
0.06
0.12
0.18
0.24
0.30
0.05
0.10
0.15
0.20
0.25
25
30
35
40
45
50
55
60
Standard length (mm)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Whole fish wet tissue weight (g)
3
6
9
12
15
Body depth (mm)

different oocyte diameters and gonad weights which affect the predicted relationships above.

Striped blenny clutch size (the number of oocytes female^{-1}) scaled non-linearly with female SL (R^2 = 0.75; Table 8; Figure 29A) and body depth (R^2 = 0.75; Table 8; Figure 29B), but had no relationship with whole fish WTW (R^2 = 0.42; Table 8; Figure 29C) or gonad WTW (R^2 = 0.61; Table 8; Figure 29D). Female striped blenny gonad WTW had no relationship with standard length (R^2 = 0.46; Table 8; Figure 28B), body depth (R^2 = 0.46; Table 8; Figure 28D), or whole fish WTW (R^2 = 0.56; Table 8; Figure 28F). Females of similar sizes may be at different gonadal stages at any given time, resulting in different gonadal weights and oocyte diameters for fishes of the same size.

Figure 29: The relationship between striped blenny (A) standard length (mm), (B) whole fish wet tissue weight (g) and (C) gonad wet tissue weight (g) and number of eggs female^{-1} for 6 females. Model coefficients are presented in Table 8.



number of oocytes female^{-1}
A
Standard length (mm)
B
Body depth (mm)
C
Whole fish wet tissue weight (g)
D
Gonad wet tissue weight (g)

DISCUSSION

Habitat use during the spawning season was temporally offset between naked gobies and striped blennies. In North Inlet, naked gobies start spawning later and for fewer weeks than striped blennies. Nest site selection is length-dependent (Crabtree and Middaugh 1982) and competition for the same nest sites may occur between naked gobies, striped blennies, and other co-occurring species with similar lengths such as the feather blenny, *Hypsoblennius hentz,* and the crested blenny, *Hypleurochilus geminatus*. The majority of male naked gobies (93%) and striped blennies (76%) were within the same standard length range (25-59 mm SL). However, body depth may be one discriminating factor that alleviates competition between species (Smith 1978; Munday and Jones 1998; Untersteggaber et al. 2014). Untersteggaber et al. (2014) observed that two sympatric coral reef gobies, *Gobion histrio* and *G. rivulatus,* had different body shapes (round vs. laterally compressed) which allowed them to occupy different coral species. Naked gobies had shorter body depths than striped blennies, which may allow them to enter shells with smaller gape widths and reduce competition for nesting habitat. Conversely, the deep-bodied and laterally compressed striped blennies may use a different range of shell gapes and sizes.

Increasing female GSI values after the start of the spawning season as water temperature and day-length increased (March through June 2013) suggests that females develop gonadal tissue in between clutches. Because female naked gobies and striped blennies do not exhibit parental care after clutch deposition they can forage between deposition events and allocate energy towards gonadal development. This strategy has been observed in other temperate goby and blenny females (e.g. *Blennius pholis*, Blenniidae; *Gobius minutus,* Gobiidae; Qasim 1956). The decline in GSI values observed after the end of the naked goby and striped blenny spawning seasons indicates that females reduced the amount of energy allocated to gonadal development.

Decreasing striped blenny male GSI values after the start of the spawning season as water temperatures increased suggests that males did not re-develop gonadal tissue to the pre-spawning levels as the spawning season progressed. Nest guarding behaviors exhibited by striped blenny males during nest development require energy and may limit the energy available for gonad development as demonstrated for other temperate species (e.g. *Gobiusculus flavescens,* Gobiidae; Skolbekken and Utne-Palm 2001). The apparent decrease in male striped blenny energetic investment directed toward gonad formation during the spawning season likely does not affect gamete production because the production of sperm requires less energy than the production of oocytes (e.g., *Zosterisessor ophiocephalus,* Gobiidae; Franco et al. 2003).

Male naked gobies and blennies increased weight at a faster rate relative to length than females. Size differences between males and females is common in demersal fishes whose males take on the dominant role in parental care (e.g., *Gobsiosoma ginsburgi*, Gobiidae; *Hypsoblennius hentz,* Blenniidae, Hildebrand and Cable 1938; *Cottus bairdi*, Cottidae, Savage 1963). Size differences between male and female naked gobies and striped blennies have been observed previously (Hildebrand and Cable 1938; Dahlberg and Conyers 1973). Females allocated more energy into gonadal development than males which may reduce the amount of energy available for somatic growth.

Naked gobies compensated for shorter spawning seasons than striped blennies by investing disproportionately more energy into reproduction than striped blennies. Clutch size and gonad weight relative to female length increased disproportionately faster for naked gobies than striped blennies. Naked gobies produced smaller oocytes at larger quantities per individual female at one point in time than striped blennies. Naked gobies are relatively smaller than striped blennies and have shorter lifespans (1-2 years) than striped blennies (3-4 years; Nero 1976; Hildebrand and Cable 1938; Able and Fahay 1998). It is beneficial for the naked goby to allocate energy into reproduction rather than somatic growth in order to produce as many offspring as possible during a single spawning season. Conversely, striped blennies exhibit a reproductive strategy in which they produce fewer oocytes per individual female at one point in time, but the oocytes are larger. Along the r-K-continuum, the naked goby is more r-selected while the striped blenny more K-selected because of their differences in clutch size and lifespan (MacArthur and Wilson 1967; Pianka 1970). Clutch size may be limited by the number of embryos the male naked goby or striped blenny can most efficiently guard from predators or keep clean from siltation (Dando 1984). Female body morphology may also limit how many oocytes are produced for each clutch (Miller 1984). The lateral compression observed in striped blennies may limit gonad size and, therefore, the number of oocytes produced (Miller 1984).

Naked gobies and striped blennies have evolved a “bet-hedging” strategy that is reflected in clutch deposition patterns (Cohen 1967). Instead of producing one clutch per year, naked gobies and striped blennies lay multiple clutches during the spawning season. Multiple clutches sequentially release larvae and increase the likelihood that some larvae will be present during suitable conditions for growth and survival to recruitment. The time between deposition events is controlled by female gonadal developmental rates which are influenced by food availability and water temperature (Trippel et al. 1997). Adult female naked gobies likely produce clutches at weekly or biweekly intervals (24-36 mm SL, Nero 1976). Striped blenny females probably have a similar clutch deposition schedule assuming food and temperature conditions are suitable.

Naked gobies may have greater annual fecundity than striped blennies despite their smaller size and shorter spawning season because they invest more into clutch size. The clutch size estimated for the largest gravid naked goby female standardized by female standard length (61 oocytes mm^{-1}) was more than six times greater than the clutch size estimated for the largest gravid striped blenny female standardized by female standard length (10 oocytes mm^{-1}). Annual fecundity, estimated using bi-weekly clutch deposition intervals, was 23,100 for the largest naked goby female observed (36 mm SL compared to 8,700 for the largest striped blenny female observed (56 mm SL). Fiorin et al. (2007) observed the annual fecundity of the temperate goby, *Gobius niger*, to be three times greater than another larger temperate goby, *Zosterisessor ophiocephalus*, that occupied the same habitat.

Striped blenny oocytes were twice the size as naked goby oocytes. Larger oocytes usually produce larger larvae that may have advantages over smaller larvae (Chambers 1997). Larger larvae are better able to resist starvation after yolk-sac absorption and have increased swimming ability which aids in foraging and predator avoidance (Hunter 1981; Miller et al. 1988)

The reduction in oocyte size observed after June in both species may be associated with the production of multiple clutches by sequential spawns. Nero (1976) observed oocytes (0.05-0.43 mm diameter) and mature oocytes (0.45-0.68 mm diameter) in Chesapeake Bay naked goby females from April to July at water temperatures of 18-29°C. Individual females never contained both developing and mature oocytes, indicating clutch-synchronous gonad development (Nero 1976). In North Inlet, female naked gobies used for oocyte-diameter measurements were collected at similar water temperatures as those collected by Nero (1976). North Inlet naked goby females also contained oocytes that were within either the "developing" or "mature" oocyte range described by Nero (1976), but not within both for any individual female. It is likely that the female naked gobies and striped blennies used for oocyte-diameter measurements in this study were at different gonadal developmental stages.

The observed variation in naked goby and striped blenny oocyte diameters during the spawning season may also be influenced by female energetics. The energetics of oocyte production may vary depending upon the clutch number and chronology within the spawning season (Chambers 1997). Egg-size varies seasonally in some fishes (e.g. *Blennius ocellaris*, Blenniidae; *Clupea harengus*, Clupeidae) with the largest eggs produced in the spring at the coolest temperatures (Bagenal 1971; Hunter 1981). Naked goby and striped blenny oocyte diameters were larger earlier in the spawning season (April-June) at water temperatures <25°C compared to oocyte diameters measured from fishes collected later in the spawning season (July-August) at 30°C. After multiple clutches, females may have less energy to invest gonad development thus producing smaller oocytes late in the spawning season (e.g., Mediterranean goby, *Zosterisessor ophiocephalus*, Zucchetta et al. 2012).

Longer breeding seasons are observed in lower latitudes because favorable water temperature and light conditions are present for longer periods of time annually (Table 1;

Qasim 1956; Johannes 1978). Naked gobies observed in Alazan Bay, Texas (27°N, Dokken et al. 1984) may spawn year round, while in Long Island, New York (41°N) naked gobies spawned for 16 weeks (Dahlberg and Conyers 1973). In North Inlet, South Carolina (33°N) naked gobies and striped blennies spawned for 21 and 30 weeks, respectively. The general trend of increasing spawning season duration with decreasing latitude has been observed for other temperate gobies with wide habitat ranges (e.g., *Gillichthyes mirabilis*, Gobiidae, De Vlaming 1972; *Asterropteryx semipunctata*, Gobiidae; Privitera 2002). The tropical goby, *Asterropteryx semipunctata*, spawns year round in the waters of Hawaii (21°N), but only for 4-5 months in the temperate waters of Japan (30-33°N, Privitera 2002).

Day-length is likely the driving factor determining the onset of the naked goby and striped blenny spawning seasons because of their wide salinity and temperature tolerances (Fritzsche 1978). The naked goby and striped blenny spawning season durations observed for 2012-2013 agree with previously reported occurrences of goby and blenny and larvae in North Inlet (Allen and Barker 1990; Allen et al. 2008). However, Allen and Barker (1990) observed naked goby and blenny larvae (unknown species) to appear in the water column at lower water temperatures (12-15°C) than those that were observed for the onset of spawning in 2012 and 2013. Allen and Barker (1990) observed naked goby larvae in the water column from April through October (26 weeks; WT = 15-30°C; salinity = 15-35) and blenny larvae from April through November (16-24 weeks; WT = 12-30°C; salinity = 15-35) during 1981-1984.

At evolutionary time scales, adult naked gobies and striped blennies have adapted their spawning season cycles to integrate annual environmental (e.g., water temperature, day-length) and trophic conditions to maximize larval production. Many other temperate and subtropical gobies and blennies exhibit annual reproductive cycles that are synchronized with environmental cues (Table 9). The spawning seasons for subtropical gobies may occur year-round because water temperature and light do not restrict breeding (Johannes 1978). In subtropical habitats, spawning events may be synchronized with other environmental factors including wet or dry seasons (e.g., *Lentipes concolor*, Gobiidae, Way et al. 1998) or lunar phase (e.g., *Ophioblennius atlanticus*, Blenniidae, Robertson et al. 1990; *Sigamus argenteus*, Siganidae, Takemura et al. 2004).

Female naked gobies and striped blennies may invest the most energy into reproductive development when food conditions are the most favorable for larvae. Lonsdale and Coull (1977) observed the highest densities of the larval fish prey, copepods (e.g. *Parvocalanus crassirostris,* Paracalanidae; *Oithona colcarva*, Oithonidae) and bivalve veligers (e.g. *Crassostrea virginica*), between April and August (WT = 20-30°C) in North Inlet. Naked goby and striped blenny larvae have been observed to feed on both copepods and bivalve veligers during laboratory feeding experiments (Harding 1999). Female GSI values for adult gobies and blennies were at their highest values from April through June which suggests that female investment into gonadal tissue and clutch production was also high during the time when planktonic food sources are at their highest densities. The end of the naked goby and striped blenny spawning seasons occurred when water temperature and day-length were optimum for growth and foraging (WT > 20°C; day-length > 11 hr). The cessation of spawning before water temperatures or day-length declined below levels that may impact larval fish growth or feeding

Table 9: Summary of spawning data for selected temperate and subtropical Gobiidae and Blenniidae. Data that were not applicable are indicated by NA. Day-length data for each location were retrieved from the U.S. Naval Observatory (usno.navy.mil). Standard length (mm) is indicated by SL.

Family	Species	Location	Water Temp. (°C)	Day-length (hr.)	Spawning season (mo.)	Max. SL (mm)	Fecundity	Method
Gobiidae	**Temperate**							
	Gobius niger[1]	Rio de Aveiro, Portugal	15-20	13.9-15.0	May-August	115	700-2,000	Ovarian batch
	Pomatoschistus Marmoratus[2]	Strymon River, Greece	NA	11.2-15.0	February-July	57	NA	NA
	P. microps[1]	Rio de Aveiro, Portugal	17-20	11.2-15.0	Mar-August	35	500-4,000	Ovarian batch
	P. minutus[1]	Rio de Aveiro, Portugal	12-20	10.0-15.0	January-August	64	1,430-4,070	Ovarian batch
	Zosterisessor ophiocephalus[3]	Venice Lagoon, Italy	10-25	12.0-15.8	March-July	150	NA	NA
	Subtropical							
	Asterropteryx semipunctata[4]	Kaneohe Bay, Hawaii	NA	11.0-13.5	January-December	46.5	131-2,210	Ovarian clutch
	Awaous guamensis[5]	Wainiha River, Hawaii	NA	13.0-13.5	May-December	207	55;716-689,500	Field nest; Ovarian batch
	Lentipes concolor[6]	Makamaka'ole Stream, Hawaii	NA	11.0-13.3	January-December	79	184-122,150	Ovarian batch
Blenniidae	**Temperate**							
	Aidablennius sphinx[7]	Corsica, France	>14	12.8-15..3	April-August	80	1-897	Lab clutch
	Hypsoblennius hentz[8]	Beaufort, NC	16-28	13.5-14.4	May-September	93	3,750	Field nest

[1]Arruda et al. (1993)
[2]Koutrakis and Tsikliras (2009)
[3]Zucchetta et al. (2012)
[4]Privitera (2002)
[5]Ha and Kinzie (1996)
[6]Way et al. (1998)
[7]Kraak (1996)
[8]Hildebrand and Cable (1938)

ensures that the last larvae produced are allowed a growth period of 2-3 weeks during optimum conditions.

Naked gobies and striped blennies present in South Atlantic Bight estuaries are temperate analogs to tropical reef fishes. North Inlet naked gobies and striped blennies do not appear to rely on a period of winter gonad conditioning that would be indicated by increases in gonadal investment (GSI values) before the initiation of the spawning season. This may be because gobies and blennies are able to migrate into deeper channels during the winter where water temperatures may be warmer. Like subtropical species, naked gobies and striped blennies in North Inlet have evolved relatively long reproductive seasons in which multiple clutches are produced. However, naked gobies and striped blennies do not spawn year round in North Inlet. Their annual reproductive cycles are synchronized with water temperature and day-length cues to co-occur with annual planktonic production cycles to ensure that their larvae are present in the water column during optimum food conditions.

CHAPTER 2:
EARLY LIFE HISTORY OF THE NAKED GOBY (*GOBIOSOMA BOSC*) AND THE STRIPED BLENNY (*CHASMODES BOSQUIANUS*)

ABSTRACT

The naked goby (*Gobiosoma bosc*) and striped blenny (*Chasmodes bosquianus*) are sympatric oyster reef fishes present within temperate estuaries. Early life history metrics including larval period duration and settlement length affect recruitment to the adult population. Larvae that settle earlier or at larger sizes reduce their exposure to planktonic risks and may be better suited for resource competition after settlement. The naked goby and striped blenny spawning seasons lasted for 21 weeks and 30 weeks, respectively, during 2012 and 2013 in North Inlet, South Carolina. Naked goby and striped blenny hatch length (mm), larval period duration (LPD, days post hatch), age-at-flexion (days post hatch), flexion length (mm), settlement length (mm), and larval growth rate (mm d^{-1}) were investigated during the 2012 and 2013 spawning seasons at North Inlet estuary ambient temperatures (21°C-30ºC). Naked goby and striped blenny average hatch length decreased by 13% and 25% from 3.00-3.60 mm TL and 3.60-4.32 mmm TL, respectively, between weeks 6 and 20 of their spawning seasons. After week 10 of their spawning seasons, both species reached the flexion stage 3 d earlier (6 days after hatch), had LPDs that were 10 d (40%) shorter than 23-30 d (goby) and 18-23 d (blenny), and had higher growth rates (+31% for naked goby, +22% for striped blenny) than larvae hatched during week 6 of the spawning season. Gobies and blennies respond to the seasonal temperature progression with early life history plasticity. Faster larval growth later in the spawning season facilitates settlement and reduces exposure to planktonic predation potentially increasing recruitment success.

INTRODUCTION

The naked goby (*Gobiosoma bosc*) and striped blenny (*Chasmodes bosquianus*) are two temperate estuarine fishes which rely on oyster reefs for shelter, nesting sites and food (Wells 1961; Dahlberg and Conyers 1973). Although adult fishes do not depend directly on living oysters for food, they rely on the biogenic structure created by living oysters for nesting habitat (Hildebrand and Cable 1938; Dahlberg and Conyers 1973). Adult goby and blenny females deposit eggs into empty articulated oyster shells and males fertilize and defend the eggs until hatch (Hildebrand and Cable 1938; Dawson 1966; Dahlberg and Conyers 1973; Nero 1976; Crabtree and Middaugh 1982). Females may deposit multiple clutches during the spawning season (Hildebrand and Cable 1938; Nero 1976).

Naked gobies and striped blennies have spawning seasons that may occur for 4-5 months in northern estuaries and as long as 6-7 months in southern estuaries (Table 1). The beginning of the naked goby and striped blenny spawning seasons along the South Atlantic Bight occurs when water temperatures exceed 18°C (Dawson 1966; Dahlberg and Conyers 1973; Nero 1976) during the spring (March-May). Spawning continues through the summer (June-August) and terminates in fall (September-November) as water temperatures decline below 20°C (Dawson 1966; Dahlberg and Conyers 1973).

Many reef fishes, including naked gobies and striped blennies, experience a planktonic larval stage that transitions into a benthic adult stage (Sale 1980; Doherty 1991; Leis 1991; 2010; Victor 1991; Figure 1). During the transition from the plankton to the benthos, several morphological and behavioral changes occur (Leis 1991, 2010). First, morphological and sensory features which are primitive at hatching develop during the planktonic phase (Leis 1991). Second, larvae are relatively small compared to juveniles and adults and must grow in both size and weight before settlement (Houde 1989; Leis 2010). Finally, the appearance of new structures (e.g., pelvic fins) and behaviors (e.g., demersal feeding) must occur before settlement (Leis 1991, 2010).

Recruitment to the benthos, and subsequently to the adult population, can be influenced by larval growth and mortality (Houde 1987, 1989; Pepin 1991), which in turn can be affected by predation, food availability, water temperature, salinity and light (Houde 1987; Houde and Zastrow 1993). Unfavorable environmental conditions or low food availability may decrease larval growth rate, resulting in extended planktonic development (Houde 1987). Longer larval periods may increase mortality due to planktonic predation (Houde 1987, 1989).

Water temperature may be the most important factor influencing larval growth (Houde 1989; Jobling 1996; Rombough 1996). Warmer water temperatures increase metabolic and growth rates (Houde 1989; Jobling 1996). Higher growth rates may be constrained by food availability (Houde 1975, 1978; McGurk 1984; Puvanendran and Brown 1999) and species-specific thermal tolerances (Jobling 1996; Rombough 1996). These constraints may establish optimal growth threshold temperatures between <0°C to 30°C, depending on species, beyond which larval growth and survivorship may decline (Pepin 1991; Jobling 1996; Rombough 1996; Munday et al. 2008). Fish usually spawn near the center of the embryonic thermal tolerance zone, and thermal tolerance increases with increasing fish age and size (Jobling 1996; Rombough 1996).

Larval fish predator avoidance and food capture may be influenced by hatch size (Chambers 1997). Longer hatch lengths might be advantageous because larvae are better able to swim and search for food (Hunter 1981). Larvae hatched at shorter lengths require increased growth rates to reach the same size-at-age as larger hatched larvae (Hunter 1981; Anderson 1988). Hatch size may be influenced by egg size, parent condition and water temperature (Hunter 1981; Chambers et al. 1989; McCormick 1999).

Growth rate may influence age- and size-at-flexion. Flexion is a critical developmental stage which leads to increased larval fish mobility for feeding and predator avoidance (Murphy and Willis 1996). Pre-flexion fishes have a notochord that is straight at the caudal tip (Murphy and Willis 1996). The flexion process begins with the dorsal bending of the notochord at the caudal peduncle and finishes when the notochord is bent perpendicular to the notochord axis (Murphy and Willis 1996). The caudal-fin rays develop further during the flexion process (Murphy and Willis 1996). Sensory abilities such as sight and olfactory perception may also further develop during flexion (Leis 2010). Changes in the timing of this developmental transition, due to increased growth rate, may benefit fast-growing larvae compared to slow-growing larvae.

Larval period duration (LPD) and settlement size are two other metrics that are influenced by growth rate that are linked to individual recruitment success (Houde 1987; Leis 1991). Fast-growing larvae might settle earlier than slow growing larvae (Victor 1991; Sponaugle et al. 2006). Shorter larval periods would reduce exposure to planktonic predators and advection processes (Victor 1986). Larval with shorter larval periods may also have priority in settlement site selection (Sale 1977, 1982). However, larvae that remain in the water column longer may settle at larger sizes (Victor 1986, 1991; Wellington and Victor 1989; Leis 1991) and may be better competitors for resources with conspecific juveniles (Leis 1991).

Recruitment occurs once a larva has settled and has survived the transition into a juvenile known as metamorphosis (Jones 1991; Leis 1991; Murphy and Willis 1996). During metamorphosis, larvae undergo body-form changes and develop adult-like coloration and behavior (Victor 1991). Metamorphosis may happen abruptly (within 24 hr) or gradually (days to weeks) depending on species (Leis 1991).

Naked gobies and striped blennies occupy estuaries along the U.S. Atlantic seaboard from New York to Florida and the Gulf of Mexico coast (Hildebrand and Cable 1938; Fritzsche 1978). Naked goby and striped blenny early life histories have been described throughout their geographic range (Table 1). The duration of their spawning seasons increases with decreasing latitude from 4-5 months in New York (Dawson 1966) to 7-8 months in the Gulf of Mexico (Dawson 1966; Dokken et al. 1984). In southeastern estuaries, naked goby and striped blenny spawning occurs from April through October between 16 and 30°C (Hildebrand and Cable 1938; Dahlberg and Conyers 1973).

The early life histories of the naked goby and the striped blenny were described during two consecutive spawning seasons in North Inlet estuary, South Carolina. Hatch lengths, settlement lengths, and larval duration were described during the spawning season as water temperature increased. Durations of the spawning seasons were estimated by monitoring nesting activity on North Inlet oyster reefs in 2012 and 2013. Hatch length (mm), flexion length (mm), age-at-flexion (days post hatch), settlement length (mm), LPD (days post hatch), and growth rate (mm d^{-1}) were determined for cultured larval fishes. Because shrinkage in preservative solutions is widely recognized (Theilacker 1980; Tucker and Chester 1984; Fox 1996; Moku et al. 2004), the change in naked goby and striped blenny larval lengths during storage in 10% Borax buffered formalin was also investigated.

METHODS

Environmental data. North Inlet, South Carolina is a tidally dominated high salinity estuary is comprised of approximately 3,200 ha of salt marsh and creeks (Novakowski et al. 2004). The estuary is characterized by three main channels branching into dozens of sub-tidal creeks, and over 1,000 intertidal creeks (Novakowski et al. 2004). The majority of North Inlet habitat is *Spartina alteniflora* dominated salt marsh (73%) with tidal creeks, mud flats, and *C. virginica* oyster reefs comprising 20.6%, 5.4% and 1%, respectively (Dame et al. 1986). North Inlet experiences an annual mean tidal range of 1.4 m and a mean tidal depth of 2.5 m (Dame et al. 1986; Novakowski et al. 2004).

An automated monitoring station at Oyster Landing in Crabhaul Creek, North Inlet records water temperature (°C) and salinity every 15 minutes (NERR CDMO; cdmo.baruch.sc.edu). Average weekly water temperatures and salinities (672 readings per week) from Crabhaul Creek were used to describe ambient conditions in the estuary from January 1, 2012 through December 31, 2013.

Nest collection and larval fish culture. Naked goby and striped blenny nests were collected during low tide from natural oyster shell 0.0-0.5 m below mean low water on North Inlet oyster reefs from May through June 2012 and April through July 2013. Nests were placed into individual 0.5 L plastic bags, and were transported to the laboratory within 2 hr of collection. Nests were considered to have hatched prematurely if they hatched during transport back to the laboratory. Premature nests were not cultured.

Nests were given unique identification numbers and placed into individual 2 L glass (2012) or plastic (2013) beakers filled with 1.5 L filtered sea-water (FSW) from Crabhaul Creek and gently aerated. The water filtration process removed particles >5 microns and was done during high tide to maintain ambient salinity (33-35) in the cultures. FSW was stored in a 120 L holding tank at ambient temperature and aerated until used (<1 wk). Daily nest water changes were made by placing the nests into clean beakers filled with FSW.

Naked goby and striped blenny larvae were placed into species-specific 2 L beakers by hatch date and nest number. The beakers were filled with 1 L FSW and aerated. Larvae were kept at initial standard densities of 50 or 100 individuals L^{-1} during 2012 and 50 individuals L^{-1} during 2013. Densities were selected for these species based on previous larval fish studies to reduce crowding and food competition (Houde 1975, 1978; Yin and Blaxter 1987; Harding 1999; Green and Fisher 2004).

Larvae were transferred to 1.5 L fingerbowls filled with 1 L FSW at 10 days post hatch (dph), where hatch = day 0, to provide more surface area for settlement. Clean empty oyster shell valves were placed into each fingerbowl to serve as settlement substrate. Water changes were made every other day for each larval culture by removing fishes with a plastic pipette and placing them into a clean beaker or fingerbowl filled with FSW. Larvae were considered to have settled when they remained perched on the bottom of the fingerbowl and their pelvic and pectoral fins were completely developed (Fritzsche 1978; Breitburg 1989, 1991). Although settled larvae had fully developed fins, they were not considered to have metamorphosed into juveniles because they had not developed adult-like pigmentation (Hildebrand and Cable 1938; Fritzsche 1978). Naked goby and striped blenny larvae may develop dorsal pigmentation within 24 h after settlement, but do not develop adult-like pigmentation until ~15 mm TL (Fritzsche 1978; Breitburg

1991). Settled larvae that were not preserved for measurement were released at Oyster Landing, Crabhaul Creek.

Fish larvae were fed a mixture of rotifers (*Brachionus plicatilis*) and 1-3 day old brine shrimp nauplii (*Artemia* sp.) 5-6 times daily from sunrise to sunset. Approximately 1,000-1,200 prey items L^{-1} were maintained in the larval fish cultures at all times to ensure that food was not limiting. Food concentrations were selected for the two species based on previous naked goby and striped blenny culture (Harding 1999) and other larval fish studies (Houde and Palko 1970; Lasker et al. 1970; Wyatt 1972; Houde 1978; Eldridge et al. 1981; Munk and Kiorboe 1985; Chesney 1989; Connaughton and Epifanio 1993; Puvanendran and Brown 1999). Rotifer concentrations were gradually decreased from 100% to 0% and brine shrimp nauplii concentrations were gradually increased from 25% to 100% based on larval fish age within each culture. Fish larvae were introduced to brine shrimp starting at 6 dph (25%) and concentrations were gradually increased at three day intervals to 100% by 15 dph. Rotifer and brine shrimp concentrations were verified daily by counting number of prey items ml^{-1}. Prey items were dispensed to larval fish cultures through pipettes. The rotifer and brine shrimp ratios were maintained by number of pipettes dispensed to each culture.

Nest and larval fish culture beakers were maintained at ambient water temperature within flow-through seawater flumes (8.4 × 0.1 m) at the University of South Carolina Baruch Marine Field Laboratory (BMFL). Water was pumped from Crabhaul Creek, North Inlet at ~200 L m^{-1}. Culture flume water temperatures (°C) were recorded daily with thermometers from June through August 2012 and with temperature loggers April through July 2013.

Preservation and measurement. A minimum of 3 larvae were removed from each culture every three days from hatch (day 0) until settlement and preserved for length measurement in 10% Borax buffered formalin. Larvae remained preserved until measurement (<150 days) and then were transferred to 70% ethanol. Total length (TL, mm) was obtained for each preserved larvae. In 2012, TL was measured using high resolution digital photographs and Image Pro software. In 2013, TL was measured using a dissecting microscope (90-250x) and stage micrometer (0.1 mm scale).

Individual larvae were identified as pre-flexion or post-flexion based on the presence/absence of the upward flexion of the notochord at the caudle peduncle (per Hildebrand and Cable 1938; Fritzsche 1978; Able and Fahay 1998). Because larvae were sampled every three days, the age-at-flexion for each larval fish culture was described using a range from 0 to 100% flexion. A classification of 0% flexion was assigned to fishes preserved at an age when no larvae sampled had undergone flexion but a proportion of larvae at the next sampled age had undergone flexion. When all larvae preserved at an age had undergone flexion, the designation was100% flexion. Flexion total length was described using the total lengths of preserved larvae within the age-class that flexion was first observed.

Larval shrinkage. In 2013, one naked goby and one striped blenny larval culture was used to determine shrinkage associated with preservation in 10% Borax buffered formalin. Three to five larvae were removed from each culture from hatch (0 dph) until 19 dph. After removal, larvae were immediately placed into 50 ml vials filled with seawater and cooled over ice to reduce movement. Larval live total length (0.1 mm) was measured using a dissecting microscope (90-250x) and stage micrometer (0.01 scale).

After measurement, larvae were preserved in 10% Borax buffered formalin and preserved total length (0.1 mm) was measured 10, 40, 60, 90, 140 and 150 d after preservation for the same larvae over time. The last remeasurement date was chosen because larvae used for growth curve descriptions did not remain in formalin longer than 150 days before being transferred to ethanol in 2012 or 2013.

Age-specific proportional change in TL on each remeasurement date was calculated by standardizing the difference between live TL and preserved TL by live TL using the equation:

$$\text{Proportional change in PTL}_t = \frac{(\text{PTL}_t\ (\text{mm}) - \text{LTL}_t\ (\text{mm}))}{\text{LTL}}$$

Where PTL is preserved total length and LTL is live total length of each larval fish measured at time *t*. The relationships between time preserved (days) and age-specific proportional change in TL (mm) were described using the linear regression:

$$\text{PTL}_t = \text{PTL}_0 + (\text{m} \times \text{x})$$

where PTL_t is the preserved total length at time (days after preservation) *t*, PTL_0 is preserved total length immediately after preservation and m is the slope of the line.

Data analyses. *A priori* significance levels for all statistical tests were alpha = 0.05. Assumptions of homogeneity of variance were tested using Levene’s test and assumptions of normality were tested with the Shapiro-Wilks test (Zar 2010). Data satisfied these assumptions unless otherwise indicated. Tukey’s pair-wise test was used as a parametric post-hoc multiple comparison test and Dunn’s test was used as a non-parametric post-hoc multiple comparison test (Zar 2010).

Naked goby and striped blenny larvae were grouped by week of the spawning season (starting from week 0). Species-specific one-way ANOVAs were used to test for differences in larval fish hatch, flexion and settlement lengths between weeks of different years (2012 and 2013). Naked goby larvae hatched during week 16 of the 2012 spawning season and week 10 of the 2013 spawning season (WT ~ 30.0°C) were tested using a one-way ANOVA with year as the factor and hatch, flexion and settlement lengths as response variables. Striped blenny larvae hatched during week 17 of the 2012 spawning season and week 15 of the 2013 spawning season (WT ~ 30.0°C) were tested using a one-way ANOVA with year as the factor and hatch, flexion and settlement lengths as response variables. There were no significant differences in naked goby or striped blenny hatch, flexion and settlement lengths between weeks within different years (Table 10). Subsequent analyses combined 2012 and 2013 data to describe naked goby and striped blenny early life history trends during the spawning season.

Hatch length. Species-specific one-way ANOVAs were used to test the differences in larval fish hatch lengths between weeks of the spawning season (WOS) with both 2012 and 2013 data combined. In 2013, naked goby and striped blenny nests were first collected during WOS 1-3, and the first hatch dates for naked goby and striped blenny larval cultures were during week 6. Naked goby larvae hatched during the first culture week (WOS 6; WT ~ 24°C) and larvae hatched during the last culture week naked gobies were hatched and successfully settled (WOS 16;WT ~30°C) were tested using one-way ANOVA with week as the factor and hatch length as response variables. Striped blenny larvae hatched during the first culture week (WOS 6;WT ~ 21°C) and larvae hatched during the last culture week striped blennies were hatched and successfully settled (WOS 20; WT ~30°C) were tested using one-way ANOVA with week as the factor and hatch length as response variables.

Table 10: Summary of statistical tests performed on cultured larval naked goby and striped blenny hatch, flexion, and settlement total lengths (TL, mm). Asterisks indicate significance at alpha = 0.05.

Species	Factor	Response	Test	df	Test statistic	p-value	Tukey test
Naked goby	Year	Hatch TL	ANOVA	7	F = 4.64	0.08	
	Year	Flexion TL	ANOVA	6	F = 1.60	0.26	
	Year	Settlement TL	ANOVA	12	F = 1.68	0.22	
	Week	Hatch TL	ANOVA	14	F = 67.6	<0.05*	wk 6 > wk 16
	Week	Flexion TL	ANOVA	9	F = 2.19	0.18	
	Week	Settlement TL	Kruskal-Wallis	1	H = 0.38	0.54	
Striped blenny	Year	Hatch TL	ANOVA	23	F = 2.40	0.14	
	Year	Flexion TL	ANOVA	12	F = 0.64	0.44	
	Year	Settlement TL	ANOVA	14	F = 0.94	0.35	
	Week	Hatch TL	ANOVA	46	F = 228	<0.05*	wk 6 > wk 20
	Week	Flexion TL	ANOVA	7	F = 0.74	0.42	
	Week	Settlement TL	Kruskal-Wallis	1	H = 14.3	<0.05*	wk 6 > wk 20

A 3-parameter exponential decay model was used to describe the trends in naked goby and striped blenny hatch and lengths (mm) during the spawning season using the equation:

$$L_t = L_0 + ae^{(-bt)}$$

where L_t is length during week t of the spawning season, L_0 is minimum length, a equals the difference between minimum and maximum lengths, and b describes curve steepness. Pearson correlations were used to describe the relationship between average water temperature (°C) during the week of hatch and naked goby and striped blenny hatch lengths (mm).

Flexion length. Species-specific one-way ANOVAs were used to test for differences in larval fish flexion lengths between weeks of spawning (WOS). Flexion lengths of naked goby larvae hatched during week 6 (WT ~ 24°C) and week 16 (WT ~30°C) and striped blenny larvae hatched during week 6 (WT ~ 21°C) and week 20 (WT ~30°C) were tested using one-way ANOVAs with week as the factor.

Settlement lengths. Species-specific one-way ANOVAs were used to test for differences in larval fish settlement lengths between weeks of spawning (WOS). Settlement lengths of naked goby larvae hatched during week 6 (WT ~ 24°C) and week 16 (WT ~30°C) and striped blenny larvae hatched during week 6 (WT ~ 21°C) and week 20 (WT ~30°C) were tested using one-way ANOVAs with week as the. A 3-parameter exponential decay model was used to describe the trends in naked goby and striped blenny settlement lengths (mm) during the spawning season. Pearson correlations were used to describe the relationship between average water temperature (°C) during the week of settlement and naked goby and striped blenny settlement total lengths (mm).

Larval period duration. Pearson correlations were used to describe the relationship between average water temperatures (°C) during the larval period (hatch to settlement) and naked goby and striped blenny LPD (dph).

Larval growth. A four-parameter logistic regression was used to estimate average daily growth rates (G, mm d^{-1}) for cultured larval naked goby and striped blenny length-at-age data using the equation from Harding and Mann (2000):

$$L_t = L_0 + \frac{a}{1 + e^{-\left(\frac{t - t_0}{b}\right)}}$$

where L_t is length (mm) at age (days post hatch) t, L_0 is hatch length (mm), a equals the difference between settlement and hatch lengths, t_0 age at the midpoint of the rise (or the time of maximum growth) and b described curve steepness. Larvae within weeks with similar growth curves (within 95% confidence intervals of each other) were combined. Early (weeks 0-9) and late (weeks 10-20) season naked goby and striped blenny growth curves were described using the logistic regression above. Average daily growth rates were calculated using the equation adapted from Houde (1989):

$$\mathrm{G}\ (\mathrm{mm\ d^{-1}}) = \frac{\mathrm{L}_t - \mathrm{L}_0}{t}$$

where L_0 and L_t are larval lengths (mm) at hatch and at the end of a larval period of t days. Pearson correlations were used to describe the relationship between average water temperature (°C) during the larval period (hatch to settlement) and naked goby and striped blenny growth rates (G, mm d^{-1}). Species-specific Pearson correlations were also used to describe the relationship between average water temperature (°C) from hatch to the time of maximum growth t_0 and age of maximum growth.

RESULTS

Environmental data. Seasonal water temperatures (WT) were within 1°C between years except during spring (Figure 3A). Average water temperature during spring (Mar-May) when fish begin spawning was 21.9±3.3°C in 2012 compared to 18.7±4.8°C in 2013. Winter (December-February), summer (June-August) and fall (September-November) water temperatures were approximately 13°C, 28°C and 20°C, respectively, for both years. Average weekly flume WT remained within 1°C of North Inlet WT during the 2013 culture period (Figure 3A). Crabhaul Creek water temperatures were used in all subsequent analyses to describe naked goby and striped blenny early life history relative to week of the spawning season.

Salinity ranged between 22.5 and 36.7 with an average of 34.5±0.7 during 2012 and 32.1±1.4 ppt during 2013. Winter salinity in 2013 was 2 lower than in 2012. Spring and summer salinity in 2013 was on average 4 lower than the salinity in 2012 (Figure 3B). The extended period of low salinity and high variability recorded in North Inlet between April and June 2013 did not affect the development of larval cultures because all larval fish cultures were reared at salinity of 33-35.

Hatch length. The naked goby spawning season lasted for 21 weeks during both years from April through the first week of September (per Chapter 1). Naked goby hatch length ranged between 2.76 mm TL and 3.60 mm TL. Naked goby hatch length was significantly longer for larvae hatched during week 6 of the spawning season compared to that for larvae hatched during week 16 (ANOVA, Table 10). In general, naked goby hatch length decreased as WOS and water temperature increased (Pearson correlation;

Table 11; Figure 30A and 30C). The exponential decay model described 50% of the observed variation in naked goby hatch length trends during the spawning season (Table 12; Figure 31A). Naked goby average hatch length decreased by 13% between WOS 6 and WOS 16. The observed hatch length decline between WOS was less than the variation observed within a single week (16%).

The striped blenny spawning season lasted for 30 weeks from March through the first week of October (per Chapter 1). Striped blenny hatch length ranged between 2.93 mm TL and 4.32 mm TL. Striped blenny hatch length was significantly longer for larvae hatched during week 6 of the spawning season compared to larvae hatched during week 20 (ANOVA, Table 10). Striped blenny hatch length decreased as WOS and water temperature increased (Pearson correlation, Table 11; Figure 30B and 30C). The exponential decay model described 82% of the observed variation in striped blenny hatch length trends during the spawning season (Table 12; Figure 31B). Striped blenny average hatch length decreased by 25% between week 6 and week 20 of the spawning season. The observed hatch length decline between WOS was greater than the within week variation which ranged between 10% and 18%.

Age and length-at-flexion. Week of the spawning season did not significantly affect naked goby flexion lengths (ANOVA, Table 10). Naked goby average flexion lengths ranged between 3.5 and 6.3 mm TL (Figure 32A and 32C). Naked goby larvae hatched later in the season during WOS 10 and 16 appeared to undergo flexion at earlier ages than larvae hatched during WOS 6-9 (Figure 33A and 33C). During WOS 10 and 16 (WT ~30.0°C), naked goby larvae began flexion as early as 6 dph (3.7 mm TL). However,

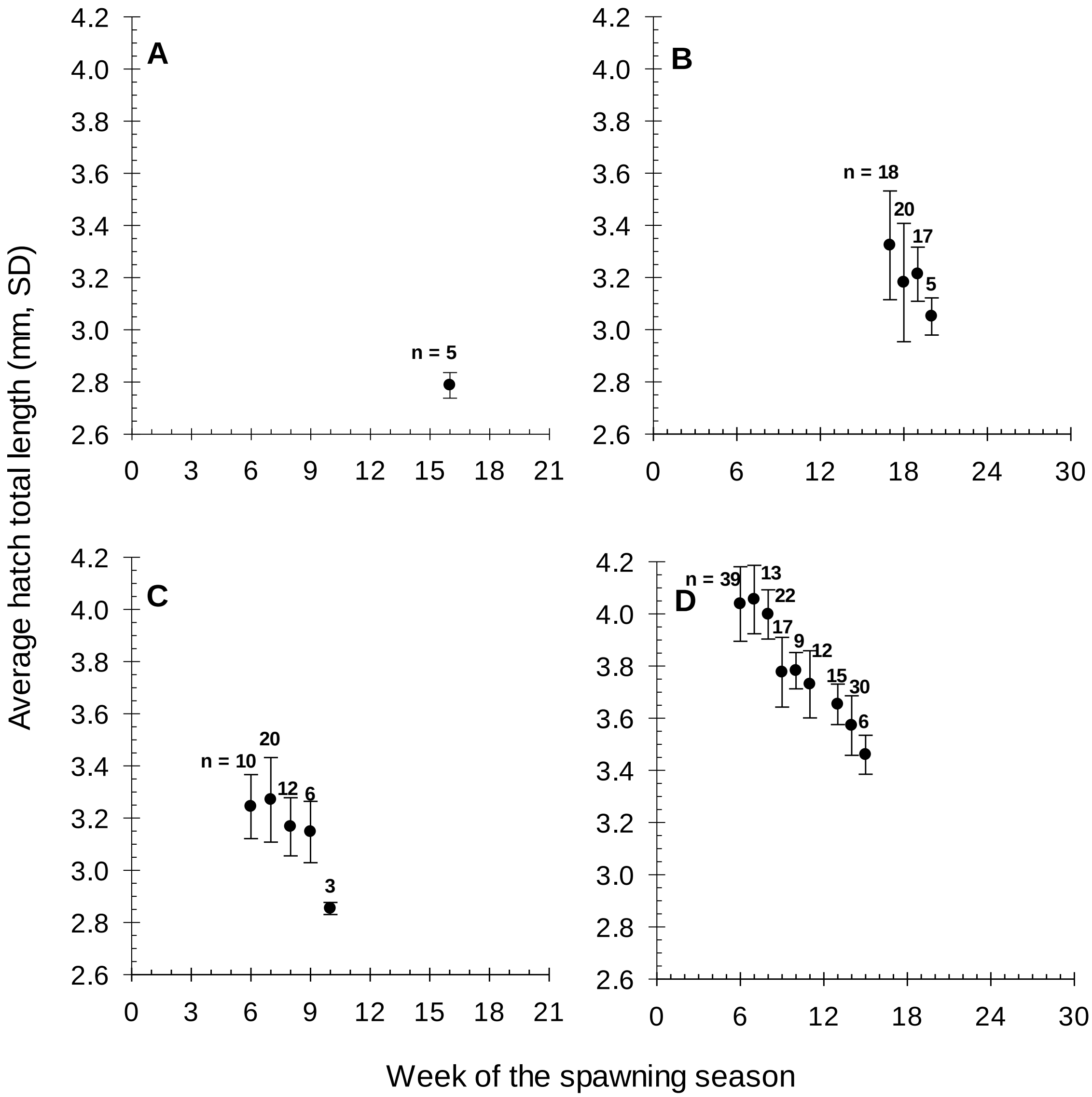
Table 11: Pearson correlation coefficients used to describe the relationships between water temperature (WT, °C) and hatch length (TL, mm), settlement length (TL, mm), larval period duration (LPD, d), average daily growth rate (mm d^{-1}), and days until time of maximum growth for cultured naked goby and striped blenny larvae. Asterisks indicate significance at the alpha = 0.05 level. n equals the number of larvae measured (hatch and settlement TL) or the number of larval cultures (LPD, growth rate, and maximum growth).

Species	Variables	n	r	p-value
Naked goby	WT vs. hatch TL	60	-0.68	<0.05*
	WT vs. settlement TL	33	-0.07	0.71
	WT vs. LPD	10	-0.51	0.14
	WT vs. average daily growth rate	6	0.78	0.07
	WT vs. age at maximum larval growth rate	6	-0.26	0.62
Striped blenny	WT vs. hatch TL	231	-0.84	<0.05*
	WT vs. settlement TL	168	-0.50	<0.05*
	WT vs. LPD	43	-0.76	<0.05*
	WT vs. average daily growth rate	13	0.18	0.55
	WT vs. age at maximum larval growth rate	13	-0.46	0.12

Table 12: Coefficients from the exponential decay model with (standard error) that were used to describe the hatch and settlement total length (TL, mm) relationships for cultured naked goby and striped blenny larvae with week of the spawning season (WOS). Model coefficients and equations are presented in the text. n equals the number of larvae that were measured.

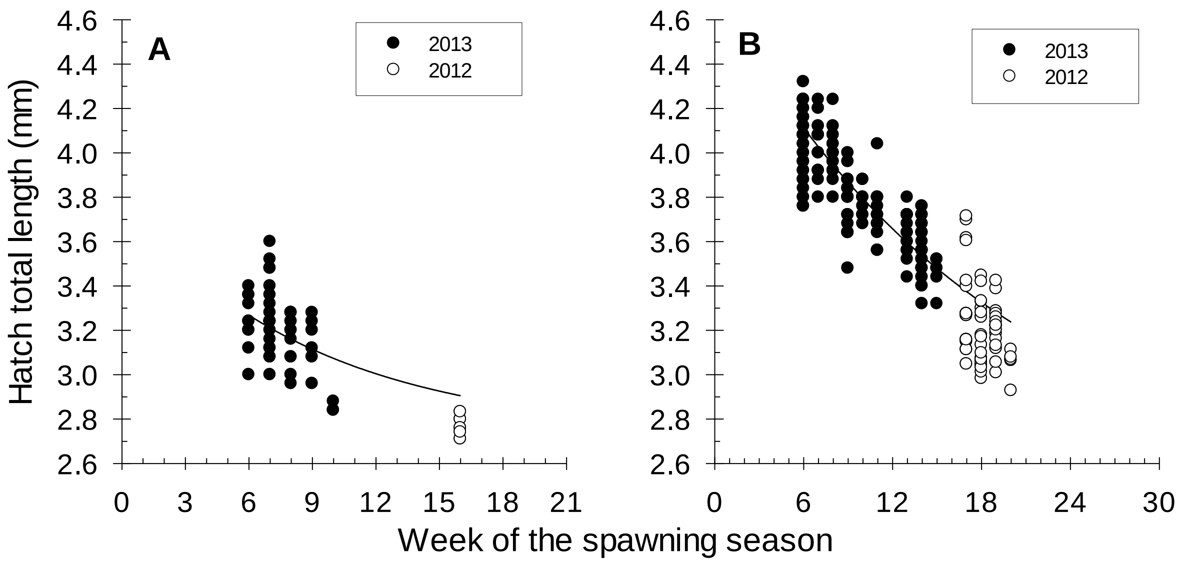
Species	Variables	n	L_0	*a*	*b*	R^2
Naked goby	WOS vs. hatch TL	60	2.55(0.41)	1.42(0.20)	0.10(0.09)	0.50
	WOS vs. settlement TL	35	7.89(1.84)	0.74(0.00)	3.29(0.00)	0.00
Striped blenny	WOS vs. hatch TL	226	2.44(0.45)	2.30(0.34)	0.05(0.02)	0.82
	WOS vs. settlement TL	172	5.79(1.47)	5.25(0.79)	0.06(0.04)	0.53

Figure 30: Average hatch total lengths (mm ± standard deviation, SD) for (A) naked goby and (B) striped blenny larvae cultured during 2012 and (C) naked goby and (D) striped blenny larvae cultured during 2013. n equals the number of larvae measured.



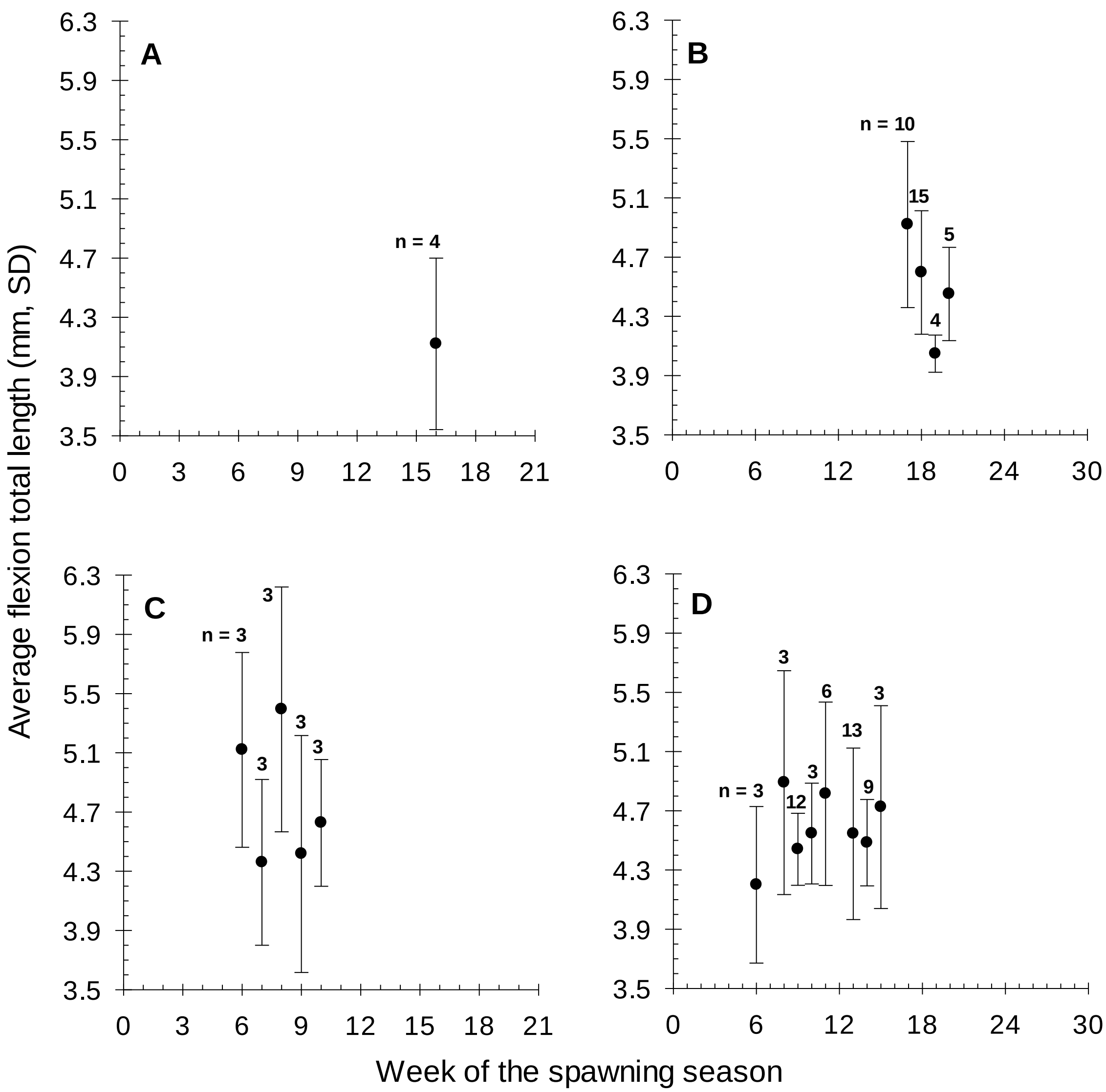
Average hatch total length (mm, SD)
A
n = 5
B
n = 18
20
17
5
C
n = 10
20
12
6
3
D
n = 39
13
22
17
9
12
15
30
6
Week of the spawning season

Figure 31: Trends in the hatch lengths (mm) for cultured naked gobies (A, n = 60) and striped blennies (B, n = 266). Coefficients for the fitted exponential curves are present in Table 11.



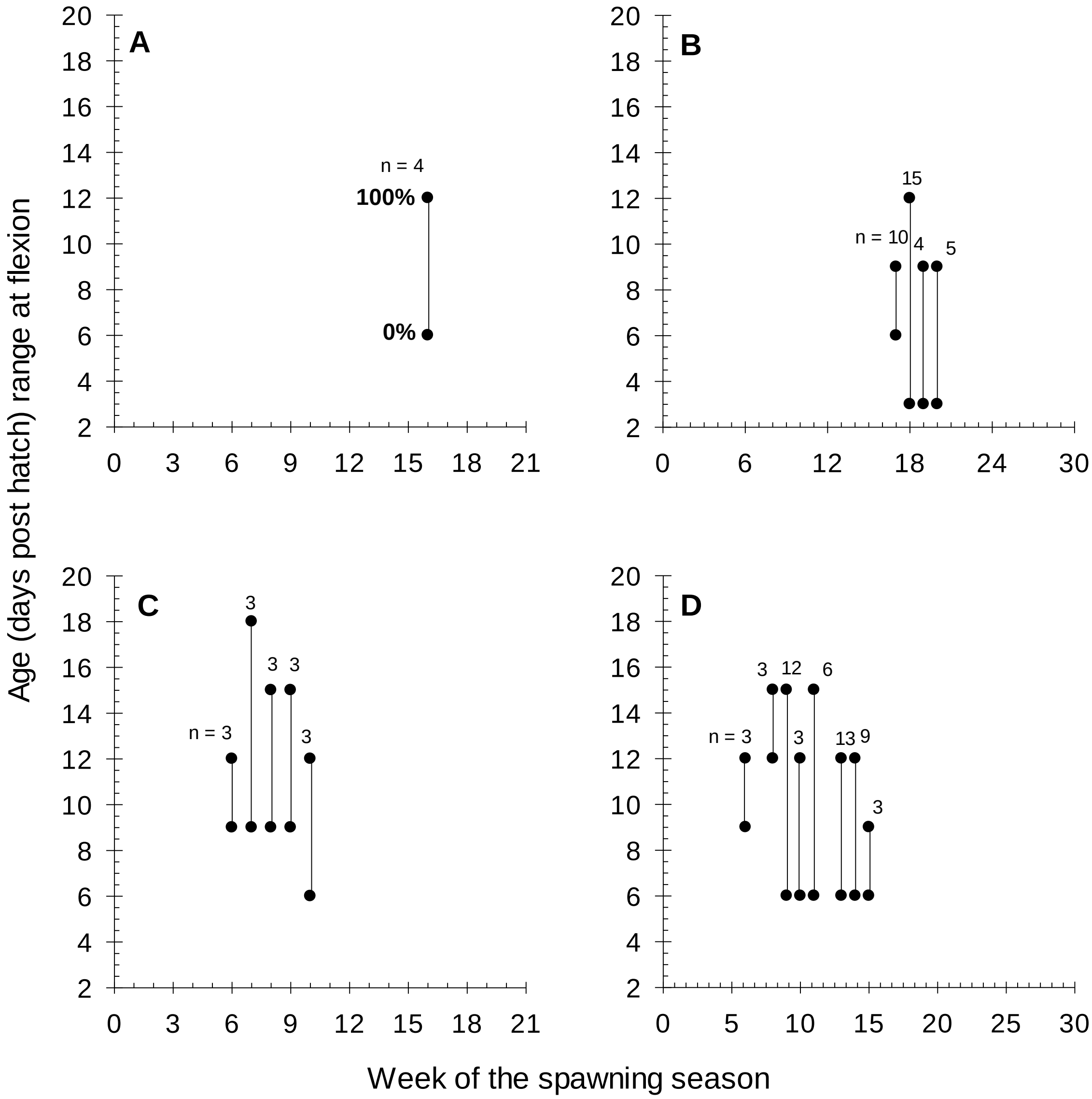
A
B
2013
2012
Hatch total length (mm)
Week of the spawning season
4.6
4.4
4.2
4.0
3.8
3.6
3.4
3.2
3.0
2.8
2.6
0
3
6
9
12
15
18
21
24
30

Figure 32: Average flexion total lengths (mm ± standard deviation, SD) for (A) naked goby and (B) striped blenny larvae cultured during 2012 and (C) naked goby and (D) striped blenny larvae cultured during 2013. n equals the number of larvae measured.



A
B
C
D
n = 4
n = 10
15
5
4
n = 3
3
3
3
3
n = 3
3
12
3
6
13
9
3
Average flexion total length (mm, SD)
Week of the spawning season

Figure 33: Age range (days post hatch) from 0% flexion to 100% flexion for (A) naked goby and (B) striped blenny larvae cultured during 2012 and (C) naked goby and (D) striped blenny larvae cultured during 2013. n equals the number of larvae measured.


A
B
C
D
n = 4
100%
0%
15
n = 10
4
5
3
n = 3
12
6
13
9
Age (days post hatch) range at flexion
Week of the spawning season

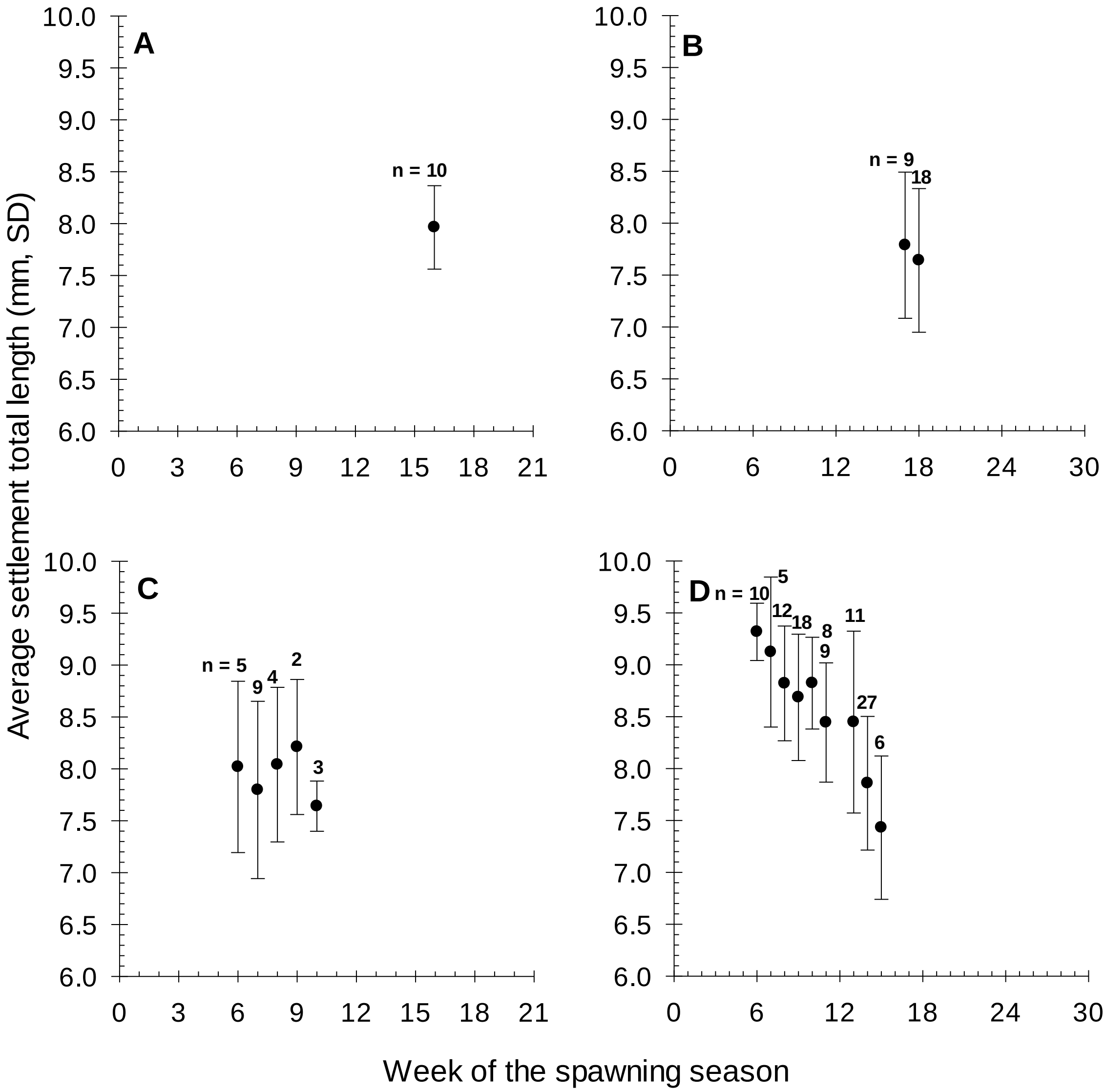
during WOS 6-9 (WT 22-28°C) goby larvae did not begin flexion until 9 dph (3.8 mm TL).

Week of the spawning season did not significantly affect striped blenny flexion lengths (ANOVA, Table 10). Striped blenny average flexion lengths ranged between 3.5 and 5.7 mm TL (Figure 32B and 32D). Striped blennies hatched later in the season during WOS 17-20 (WT ~30.0°C) began flexion as early as 3 dph (3.7 mm TL; Figure 33B). However, striped blenny larvae did not begin flexion earlier than 9 dph (3.8 mm TL) during WOS 6 (WT ~21.0°C), or earlier than 6 dph (3.8 mm TL) during WOS 8-15 (WT 22-30°C; Figure 33D).

Settlement length. Naked goby settlement lengths ranged between 6.0 and 9.0 mm TL throughout the spawning season (Figure 34A and 34C). Week of the spawning season did not significantly affect naked goby settlement lengths (ANOVA, Table 10). There was no correlation between naked goby settlement lengths and average water temperature during the larval period (Pearson correlation, Table 12).

Striped blenny settlement lengths generally decreased throughout the spawning season (Figure 34B and 34D). Striped blenny average settlement length decreased by 26% between week 6 and week 20 of the spawning season. Striped blenny settlement lengths varied between 11% and 30% within the same WOS. Striped blenny settlement lengths were negatively correlated with average water temperature during the week of settlement (Pearson correlation, Table 11). Striped blenny larvae hatched during week 20 had significantly shorter settlement lengths than larvae hatched during week 6 (ANOVA, Table 10). The exponential decay model described 53% of the observed variation in

Figure 34: Average settlement total lengths (mm ± standard deviation, SD) for (A) naked goby larvae and (B) striped blenny larvae cultured during 2012 and (C) naked goby and (D) striped blenny larvae cultured during 2013. n equals the number of larvae measured.


Average settlement total length (mm, SD)
A
n = 10
B
n = 9
18
C
n = 5
9
4
2
3
D
n = 10
5
12
18
8
9
11
27
6
Week of the spawning season

striped blenny settlement length trends during the spawning season (Table 12, Figure 35B).

Larval period duration. Naked goby LPD ranged between 19 dph and 30 dph during the culture period. Naked goby average LPD decreased during the culture period relative to week of the spawning season (Figure 36A and 36C). Average LPD decreased from 28±3.5 (n = 2, WOS 6) to 21 (n = 1, WOS 16). However, there was no correlation between naked goby LPD and average water temperature during the larval period (Pearson correlation, Table 11).

Striped blenny LPD ranged between 14 dph and 23 dph during the culture period. Striped blenny average LPD decreased during the culture period relative to week of the spawning season (Figure 36B and 36D). Average LPD decreased from 21±1.0 (n = 3, WOS 6) to 15 (n = 1, WOS 20). Striped blenny LPD was negatively correlated with average water temperature during the larval period (Pearson correlation, Table 11).

Larval shrinkage. Naked goby larvae lost between 0 and 32% of their live TL during preservation in 10% Borax buffered formalin for 150 d (Figure 37A). Striped blenny larvae lost between 0 and 16% of their live TL during preservation for 150 d in 10% Borax buffered formalin (Figure 37B). Shrinkage appeared to be independent of age for both fishes (Appendices 11 and 12). The proportion of shrinkage varied between individual fish in the same age class. Because the sample sizes were small (n < 6), the true range of variation could not be determined. The observed ranges prevented species-specific length-correction from being estimated confidently. Therefore, the length-at-age data used to estimate larval growth rates were not corrected for shrinkage.

Figure 35: Trends in the settlement lengths (mm) for cultured naked gobies (A, n = 35) and blennies (B, n = 173). Coefficients for the fitted exponential curves are present in Table 11.

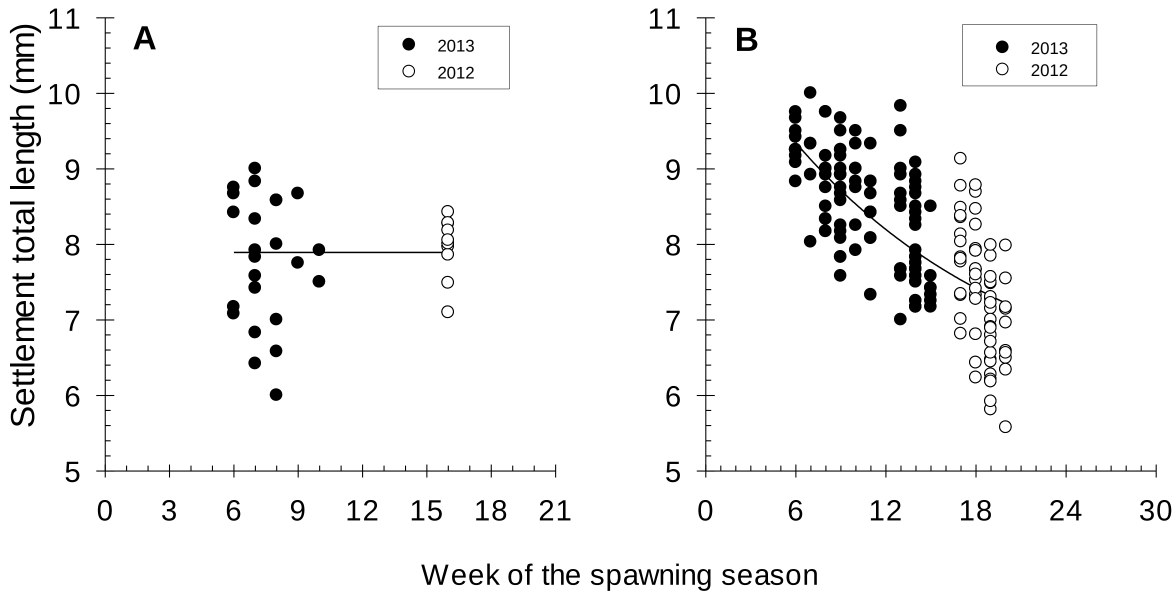
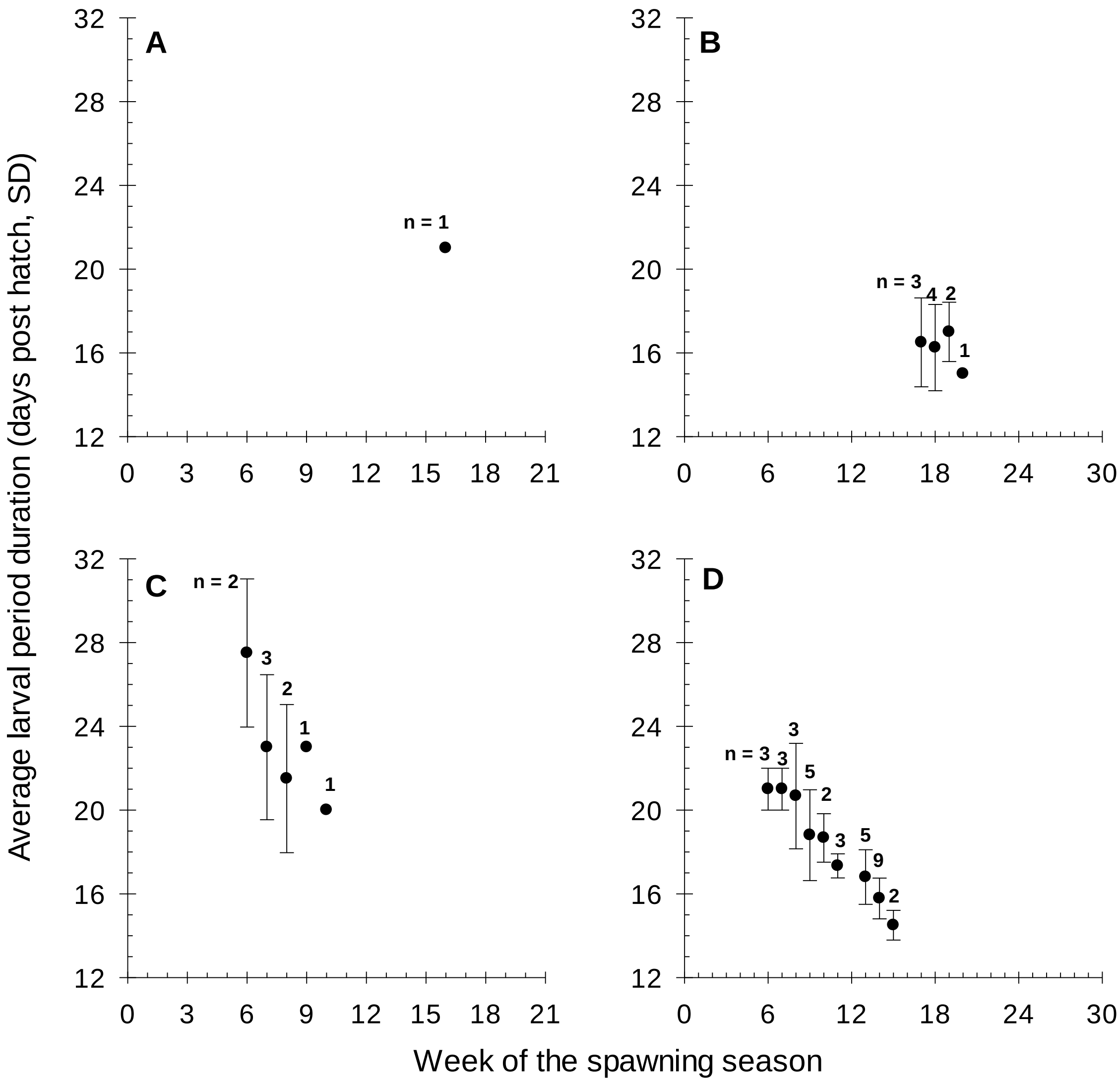
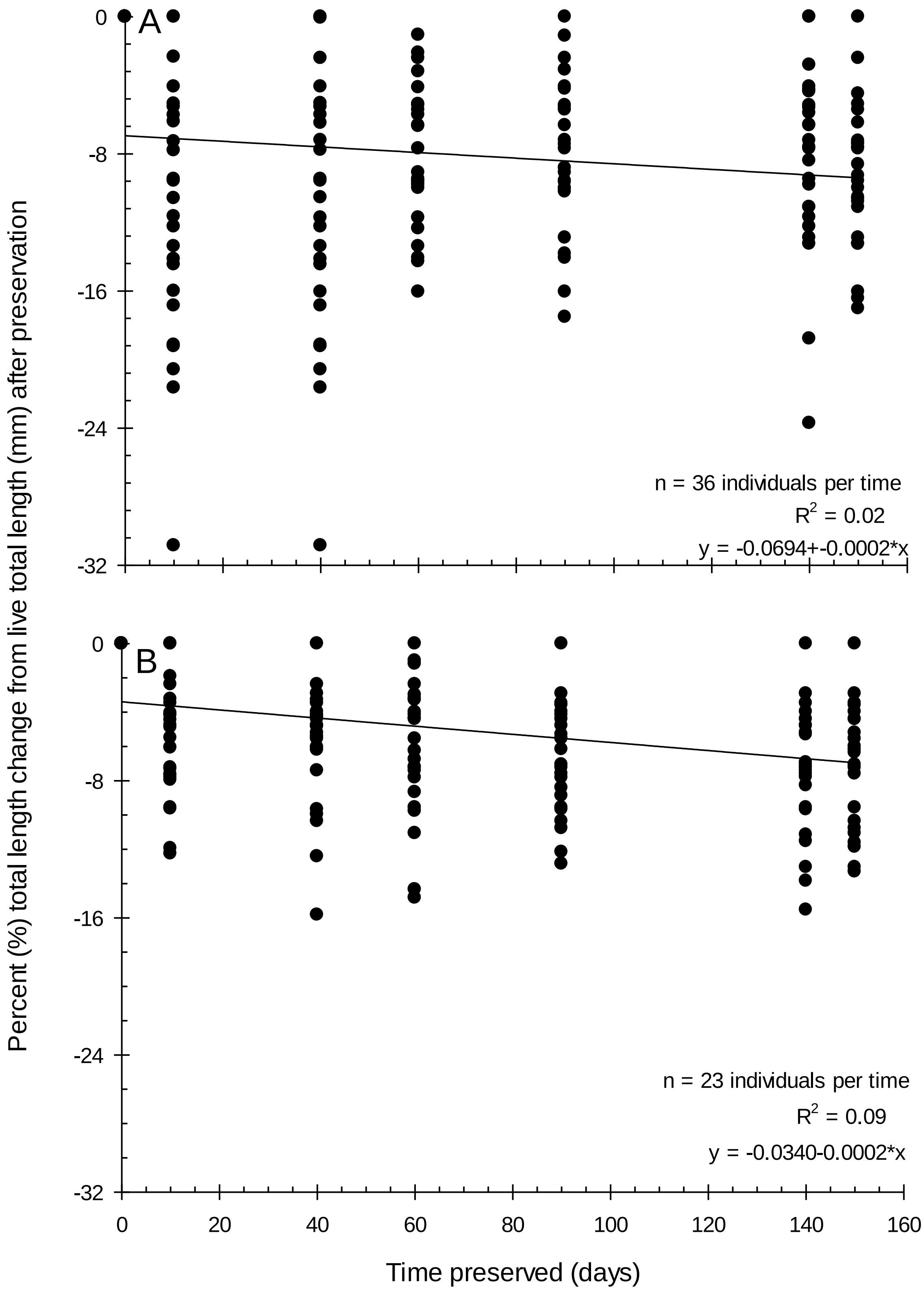

A
B
2013
2012
Settlement total length (mm)
Week of the spawning season

Figure 36: Average larval period duration (days post hatch ± standard deviation, SD) for (A) naked goby and (B) striped blenny larval cultures during 2012 and (C) naked goby and (D) striped blenny larval cultures during 2013. n equals the number of larval cultures.



A
B
C
D
n = 1
n = 3
4
2
1
n = 2
3
2
1
1
n = 3
3
3
5
2
3
5
9
2
32
28
24
20
16
12
0
3
6
9
12
15
18
21
0
6
12
18
24
30
Average larval period duration (days post hatch, SD)
Week of the spawning season

Figure 37: Percent (%) total length (mm) change from live total length (mm) for (A) naked goby 0-15 dph and (B) striped blenny 0-19 dph larvae after in 10% Borax buffered formalin.


Percent (%) total length change from live total length (mm) after preservation
A
n = 36 individuals per time
R^2 = 0.02
y = -0.0694+-0.0002*x
B
n = 23 individuals per time
R^2 = 0.09
y = -0.0340-0.0002*x
0
-8
-16
-24
-32
0
20
40
60
80
100
120
140
160
Time preserved (days)

Larval growth. The logistic model described naked goby and striped blenny larval growth during the spawning season (Table 13). Naked goby growth rates were highest (0.23 mm d^{-1}) during WOS 10 (WT ~30.0°C). Naked goby growth curves were combined for weeks 6-9 (early) and 10-16 (late) because predicted growth curves during these weeks were within the 95% confidence intervals of each other (see methods). These models showed a decrease in predicted naked goby hatch lengths and increased growth rates for fishes hatched later in the season (Table 14; Figure 38A and 38C). Neither growth rates (G) nor age of maximum growth were significantly correlated with water temperature for naked gobies (Pearson correlation, Table 11).

Striped blenny growth rates were highest (0.29 mm d^{-1}) during WOS 10 (WT ~26°C). Growth rates were also high (0.28 mm d^{-1}) later in the spawning season during WOS 15-17 (WT ~30.0°C; Table 13). Striped blenny growth curves were combined for weeks 6-9 (early) and 15-17 (late) because predicted growth curves during these weeks were within the 95% confidence intervals of each other (see Methods). These models showed a decrease in predicted striped blenny hatch lengths and settlement lengths for fishes hatched later in the season (Table 14; Figure 38B and 38D). Neither growth rates (G) nor age of maximum growth were significantly correlated with water temperature for striped blennies (Pearson correlation, Table 11).

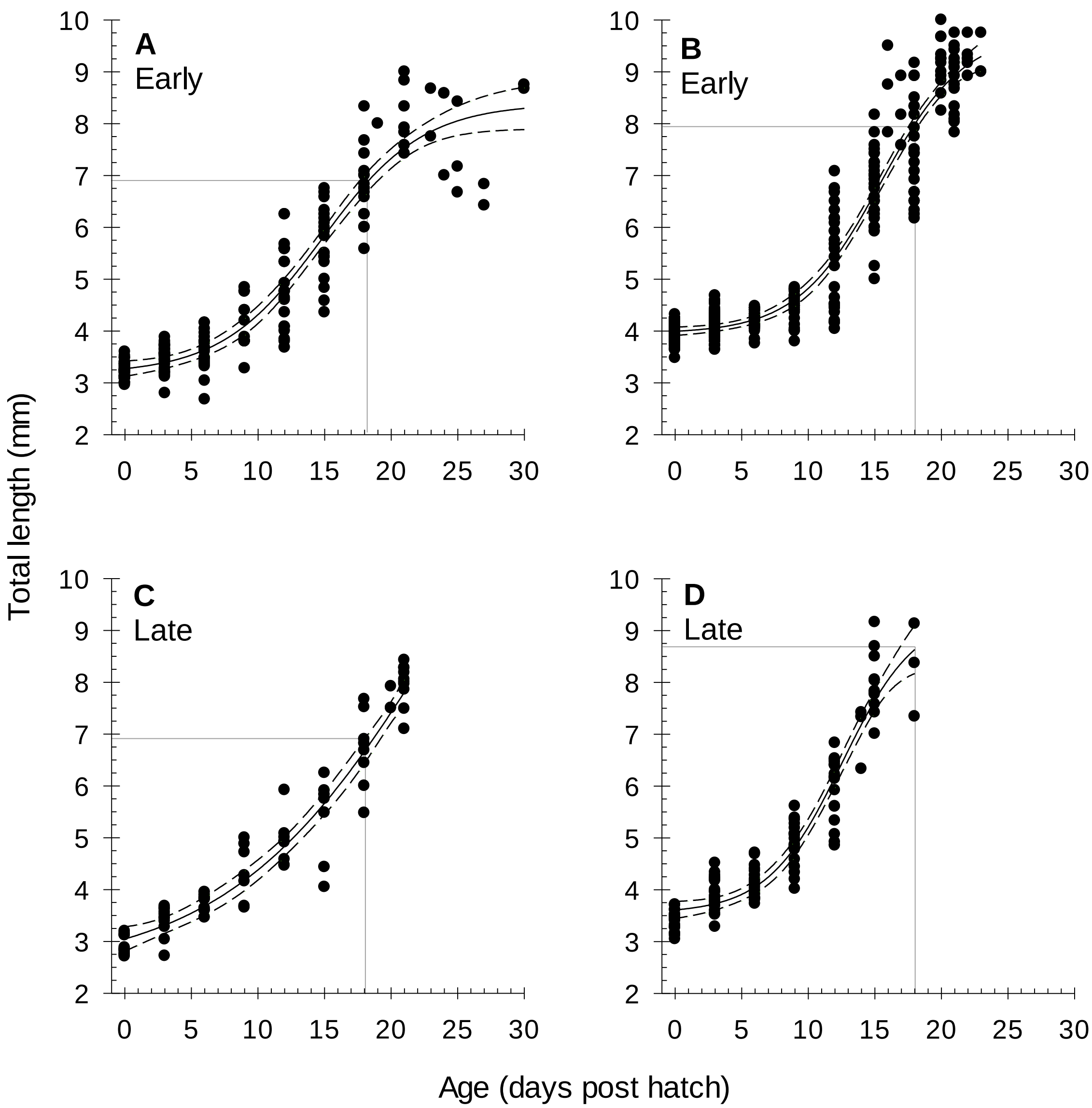
Table 13: Coefficients from the three-parameter logistic regression with (standard error) that were used to estimate average daily growth rates (G) for cultured naked goby and striped blenny larvae during each week of the spawning season (WOS). Model coefficients and equations are presented in the text. n equals the number of larvae that were measured.

Species	WOS	n	L_0		a		t_0		b		R^2	G ($mm\ d^{-1}$)
Naked goby	6	24	3.12	(0.28)	7.03	(1.68)	22.5	(2.31)	5.55	(2.35)	0.97	0.18
	7	94	3.38	(0.11)	4.53	(0.37)	14.6	(0.55)	2.80	(0.47)	0.88	0.16
	8	53	2.96	(0.26)	5.64	(0.89)	14.4	(1.14)	4.28	(1.12)	0.90	0.20
	9	25	3.13	(0.31)	5.87	(1.58)	15.8	(2.41)	4.27	(1.82)	0.91	0.21
	10	33	2.24	(0.88)	9.28	(6.71)	17.6	(8.24)	7.21	(4.30)	0.95	0.23
	16	43	3.11	(0.26)	5.99	(1.93)	16.3	(1.28)	3.89	(1.52)	0.93	0.21
Striped blenny	6	108	3.99	(0.07)	6.17	(0.48)	15.2	(0.64)	3.34	(0.45)	0.96	0.25
	7	53	3.89	(0.19)	6.10	(1.12)	15.4	(1.34)	3.87	(1.10)	0.93	0.23
	8	90	4.05	(0.07)	5.35	(0.30)	15.2	(0.39)	2.55	(0.31)	0.94	0.22
	9	108	3.76	(0.15)	5.56	(0.71)	14.8	(0.84)	3.08	(0.63)	0.87	0.23
	10	58	3.71	(0.20)	10.9	(1.07)	19.2	(3.50)	4.28	(4.88)	0.93	0.28
	11	69	3.77	(0.11)	7.00	(1.61)	15.5	(1.42)	2.97	(0.62)	0.94	0.27
	13	101	3.65	(0.19)	8.19	(4.10)	17.0	(3.13)	3.30	(1.05)	0.79	0.26
	14	193	3.68	(0.08)	6.12	(0.94)	14.4	(0.40)	2.66	(1.05)	0.90	0.26
	15	35	3.55	(0.24)	9.10	(0.77)	15.4	(5.19)	3.40	(1.44)	0.93	0.28
	17	80	3.47	(0.91)	5.57	(0.66)	12.2	(0.91)	2.76	(0.91)	0.91	0.28
	18	118	2.90	(0.44)	5.72	(1.30)	10.8	(1.26)	4.36	(1.34)	0.82	0.24
	19	90	3.20	(0.19)	4.82	(0.95)	13.0	(1.34)	3.92	(0.97)	0.91	0.21
	20	35	3.22	(0.43)	5.01	(3.13)	12.3	(3.88)	3.37	(2.23)	0.85	0.22

Table 14: Coefficients from the logistic regression with (standard error) that were used to describe changes in early and late season growth for cultured naked goby and striped blenny larvae during each week of the spawning season (WOS). Model coefficients and equations are presented in the text. n equals the number of larvae that were measured.

Species	Period	n	L_0		*a*		t_0		*b*		R^2	G ($mm\ d^{-1}$)
Naked goby	Early	175	3.24	(0.10)	4.98	(0.28)	14.6	(0.42)	3.46	(0.40)	0.89	0.16
	Late	76	2.99	(0.22)	5.84	(1.01)	15.1	(1.32)	4.17	(1.00)	0.92	0.22
Striped blenny	Early	359	3.97	(0.05)	5.75	(0.30)	15.4	(0.37)	3.06	(0.27)	0.92	0.23
	Late	125	2.80	(0.43)	7.83	(4.00)	16.5	(5.08)	6.08	(2.36)	0.89	0.24

Figure 38: Fitted three-parameter logistic regressions (black lines) with 95% confidence intervals (dashed lines) for early season cultured naked goby (A = WOS 6-9, n = 175) and striped blenny (B = WOS 6-9, n = 359) larvae and late season cultured naked goby (C = WOS 10-16, n = 76) and striped blenny (D = WOS 15-17, n = 126) larvae. Grey lines indicate predicted total lengths (mm) at 18 days post hatch. Coefficients for the logistic regressions are presented in Table 14.



A
Early
B
Early
C
Late
D
Late
Total length (mm)
Age (days post hatch)
2
3
4
5
6
7
8
9
10
0
5
10
15
20
25
30

DISCUSSION

Several early life history metrics (e.g., hatch length, age-at-flexion, settlement length, larval period duration, growth rate), and the plasticity observed in these metrics, differed between naked gobies and striped blennies. Naked gobies hatched at smaller lengths and had relatively slower growth rates than striped blennies. Naked goby larval period durations were approximately one third longer than striped blenny larval period durations. Both species settled after attaining at least 6.0 mm total length. As water temperature exceeded 28°C after week 10 of the spawning season, naked goby growth rate increased by 22% from 0.18 mm day^{-1} during week 6 (24°C), while striped blenny growth rate increased by 11% from 0.25 mm day^{-1} during week 6 (21°C). Both naked goby and striped blenny larval hatch length and larval period duration decreased and larval growth rate increased during the spawning season.

Larvae hatched later in the spawning season grew faster and reached flexion at younger ages than their early-season counterparts, but at the same total length. These observations agree with those reported by Fuiman et al. (1998) for two other laboratory reared temperate fishes (*Brevoortia tryannus*, Clupeidae; *Sciaenops ocellatus*, Sciaenidae). Flexion occurs after a minimum length threshold (Fuiman 1994; Fuiman et al. 1998). The minimum flexion lengths observed in this study were within the range previously reported for naked gobies and striped blennies (3.7-3.8 mm TL; Hildebrand and Cable 1938; Fritzsche 1978). It is likely that fishes hatched late in the spawning season at warmer water temperatures rely on fast growth to reach flexion earlier, which may facilitate successful settlement and recruitment. Larval fish swimming and prey capture ability increases after larvae reach flexion (Fuiman 1994; Fuiman et al 1988).

The transition from planktonic to benthic habitats comes with both physiological stress and ecological risk. Successful recruits have descended from the plankton, investigated locations, and experienced the process of metamorphosis (Breitburg 1989, 1991; Sweatman and St. John 1990). Reductions in larval period duration reduce exposure to risks including advection, competition for patchy planktonic food resources, and planktonic predators (Victor 1986; Houde 1987, 1989). Reduced larval periods may shorten exposure to some planktonic fish predators present in North Inlet, SC, such as the Atlantic silverside, *Menidia menidia* (Allen et al. 1995). However, immediately after settlement both naked gobies and striped blennies may be vulnerable to a different suite of benthic predators (e.g., blue crab *Callinectes sapidus)* due to their small sizes.

Competition for habitat space and nesting sites may be relevant for demersal tidal creek fishes including naked gobies and striped blennies. Suitable hard bottom substrate may be limiting in temperate estuaries much like on tropical coral reefs (Dame et al. 1986). Therefore, when sites become available through the death or migration of the previous resident fish, the first larvae to settle may retain the newly opened site (Sale 1978; Mapstone and Fowler 1988). By this mechanism, multiple species that are present in the same geographic area, such as naked gobies and striped blennies, are able to coexist because resource availability is random over space and time and any fish larvae has an equal chance of settling within an open space (Sale 1978).

Settlement size may also play an important role in larval recruitment. Fish larvae that remain planktonic longer may attain larger settlement sizes (Wellington and Victor 1989; Victor 1991). Both naked gobies and striped blennies settled at lengths above the observed settlement length threshold of 6.0 mm total length by remaining in the plankton longer than their respective shortest larval durations. Larger settlement lengths may provide a competitive advantage to juveniles for space and food resources during and immediately after recruitment (e.g., winter flounder, *Pseudopleuronectes americanus*, Chambers and Leggett 1987; naked goby, *Gobiosoma bosc*, Breitburg 1989; goldspot goby, *Gnatholepis thompsoni*, Sponaugle and Cowen 1994). While space may be an important factor determining the settlement strategies of larval fishes, different settlement strategies may facilitate variable settlement lengths (Sale et al. 1980).

Sale et al. (1980) described three settlement strategies that tropical reef fishes (Pomacentridae) exhibited when settling onto coral reef areas occupied by several similar territorial species. Sale et al. (1980) observed tropical reef fish larvae to settle along the borders outside of resident territories, colonize new reef patches, or infiltrate existing territories by remaining outside of resident reach. Larvae that exhibit the last strategy take advantage of small crevices that are too small for adults to enter. When the small recruits outgrow the small crevices, they have attained a size which would allow them to successfully compete with conspecific residents. Like coral reefs, oyster reefs provide living heterogeneous habitat, and these settlement strategies may be applicable to temperate fringing oyster reefs along the South Atlantic Bight. Variable settlement sizes may offer different advantages in avoiding post-recruitment predation. Small recruits would be able to hide in small crevices impenetrable by predators, while larger recruits may be able to escape faster (Bailey, 1984; Bailey and Batty 1984).

The negative relationship observed between naked goby and striped blenny hatch lengths and water temperatures may relate to seasonal clutch deposition patterns of parent females. Larval hatch-size has been positively related to egg-size (Hunter 1981). Egg-size has been observed to vary seasonally in some fishes (e.g. *Blennius ocellaris*, Blenniidae; *Clupea harengus*, Clupeidae) with the largest eggs produced in the spring at the coolest temperatures (Bagenal 1971; Hunter 1981). Eggs at the beginning of the season may have more yolk than eggs later in the season, thus producing larger larvae (Hunter 1981). Naked goby and striped blenny oocytes appear to develop synchronously between each clutch (per Chapter 1; Nero 1976). Synchronous females that deposit multiple clutches during a spawning season typically have more energy to invest in egg development before their first spawn than between sequential spawns, thus producing larger eggs earlier in the spawning season (e.g., capelin, *Mallotus villosus*, Chambers et al. 1989; red drum, *Sciaenops ocellatus*, Fuiman and Ojanguren 2011; Mediterranean goby, *Zosterisessor ophiocephalus*, Zucchetta et al. 2012).

Larger larvae are more resilient to starvation after yolk-sac absorption and may have increased swimming speeds that enable them to search for food over greater volumes of water (Hunter 1981; Miller et al. 1988). Such advantages would be beneficial for larvae hatched during the beginning of the spawning season at cooler water temperatures when the timing of first larval fish hatch and seasonal increase of planktonic production cycles are critical for larval fish feeding and survival. Conversely, small larvae usually have smaller yolks and may be more susceptible to starvation after yolk-sac absorption (May 1974). However, naked goby and striped blenny larvae are generalist predators that co-occur with several planktonic prey items (e.g., copepods, bivalve veligers; Harding1999) that are present March-September in North Inlet, SC (Lonsdale and Could 1977). Lonsdale and Coull (1977) observed bivalve veliger and copepod densities in North Inlet estuary to annually range between 1,000 and 30,000 L^{-1}

and between 3,000 and 90,000 L^{-1}, respectively. These estimates are well above the 1,000 prey L^{-1} feeding densities described for larval fishes reared in the laboratory (Houde and Palko 1970, Lasker et al. 1970, Wyatt 1972; Connaughton and Epifanio 1993).

Observed naked goby and striped blenny hatch and settlement lengths agree with those previously reported in other studies (Table 1). However, shrinkage in length was observed for both naked gobies and striped blennies ranging in age from hatch to settlement after preservation. The amount of shrinkage varied between individual larvae (0-32 %, goby; 0-16%, blenny) that resulted in the inability to confidently calculate length-correction factors for either species. The greatest amount of shrinkage occurred within the first 10 days of preservation for both gobies and blennies, but larval expansion occurred for some larvae after 60 days of preservation. Shrinkage within the first 10-30 days followed by larval expansion has been observed in other larval fish shrinkage studies (e.g., *Paralichthys lethostigma,* 9.48-13.05 SL, Tucker and Chester 1984; *Clupea harengus,* 9-19 mm TL, Fox 1996). The wide range of variation within the same larval age class might be caused by an individual sensitivity to preservative. Shrinkage is species (Fey 1999) and size (Fey and Hare 2005) specific. It is also likely that other factors might influence shrinkage such as muscle tissue or skeletal rigidity (Theilacker 1980). Because shrinkage did not appear to be dependent on larval age, growth rate estimates were likely not affected for either naked gobies or striped blennies.

Larval biology sets the input for fish populations through recruitment. The reproductive strategies exhibited by some tropical and temperate reef fishes include multiple clutches of eggs deposited over a prolonged spawning season (Dando 1984; Houde 1989). The naked goby and striped blenny spawning seasons lasted for 21 weeks and 30 weeks, respectively during 2012 and 2013. Optimal day-length (> 12 hr) and food availability allow for longer spawning seasons in tropical and temperate areas (Johannes 1978). The availability of recruitment space may be one pressure that favors a prolonged spawning season in reef fishes (Sale 1977, 1982; Sale et al. 1980). Prolonged spawning seasons increase the chances of larvae being the first to occupy a newly available space. Disturbances may also favor a prolonged spawning season in temperate (Dando 1984) and tropical (Johannes 1978) reef fishes. Estuarine habitats are vulnerable at centurial time scales to anthropogenic disturbance and at geologic time scales to natural coastal processes. Disturbance events (e.g., wave action) can change the availability of clean oyster shell and associated crevices (Breitburg 1992; Livingston et al. 1999; Kimbro and Grolshoz 2006). Such changes will affect the living spaces available to demersal fishes (Sano et al. 1987). Prolonged spawning seasons ensure that planktonic larvae are present in the water column during optimal environmental conditions for survival and recruitment (Johannes 1978).

Generalist demersal fishes like the naked goby and striped blenny are adapted to life in estuarine habitats. These fishes have wide physiological tolerances, widespread geographic ranges, and are opportunistic feeders (Hildebrand and Cable 1928; Fritzsche 1978). Success in estuaries may result from plasticity within the broader life history plan. Both naked gobies and striped blennies had faster growth rates and shorter larval period durations later in the spawning season. Shorter larval periods allowed naked gobies and striped blennies to attain the minimum flexion and settlement lengths earlier, thus reducing their exposure to planktonic predators despite their smaller hatch size.

SYNTHESIS

Naked gobies and striped blennies use estuarine habitats at different spatial and temporal scales throughout their life histories. The observed offsets in habitat use by adults and larvae reduce resource competition between these sympatric species. Adult nesting habitat (benthic) is partitioned on the basis of the onset of spawning, the duration of the spawning season, and oyster shell morphology (e.g., gape; Crabtree and Middaugh 1982). Differences in the timing of spawning influence the larval supply to the plankton. Once in the plankton, species-specific differences in larval size at hatch, growth rates, and larval period duration further differentiate the realized niche for each species.

The differences observed in the timing and duration of adult striped blenny and naked goby spawning season reduce overlap in benthic nesting habitat use and larval production. Striped blennies established nest sites and initiated spawning before naked gobies. The temporal offset in adult nesting activity translates into temporal offsets in planktonic habitat use. Naked goby and striped blenny larvae co-occur in the plankton at different developmental stages throughout their spawning seasons.

Ontogenetic changes in food use may occur within and between species during the planktonic phase (Hunter 1981; Govoni et al. 1983; Houde and Shektor 1980; Olney 1996). Larval fish mouth width and gape influence prey consumption (Hunter 1981). Striped blenny larvae which were larger at hatch than naked goby larvae and have sub-terminally positioned mouths may prey a different size-range of prey items than larval naked gobies which have superior positioned mouths (Hildbrand and Cable 1938). Larger larval fish may also be able to catch, subdue, and consume larger prey (Hunter 1981; Govoni et al. 1986).

In addition to the size of larvae, changes in the swimming ability and distribution of larvae within the water column prior to settlement may offset the dietary preferences of older naked goby and striped blenny larvae with younger larvae (Houde and Lovdal 1984; Breitburg 1991; Olney 1996). As swimming ability and visual acuity increases during development, it is likely that older larvae will use different areas of the water column than younger larvae (Breitburg 1989, 1991; Olney 1996). Olney (1996) described ontogenetic shifts in the vertical distributions and diet of seaboard gobies in the Chesapeake Bay. Older postflexion (> 9 mm TL) seaboard gobies were observed near the bottom of the water column and fed on predominantly copepod nauplii while preflexion (< 4.4 mm TL) seaboard gobies fed predominantly on bivalve veligers near the surface of the water (Olney 1996). Breitburg (1989, 1991) observed similar diet shifts to copepod nauplii when larval naked gobies exhibited demersal schooling prior to settlement. Striped blenny larvae may also exhibit similar behaviors and investigate settlement locations before settlement. Hettler and Chester (1990) did not observe striped blenny larvae >3.7 mm TL within their ichthyoplankton samples collected 0.5 m from the surface which suggests that larger striped blenny larvae may change their position within the water column as they grow. Both Allen and Barker (1990) and Olney and Bohlert (1988) collected larval *Gobiosoma* and Blenniidae species within 0.5 m of the benthos. The large size ranges observed for *Gobiosoma* (1.8-18.4 mm TL) and Blenniidae (1.4-17.8 mm TL) suggests that both preflexion and postflexion larvae may be present near the bottom (Allen and Barker 1990) and that distribution within the water column may change with ontogeny as well as on diel scales (Olney 1996).

Benthic habitat is spatially partitioned on temperate oyster reefs due to differences in fish body morphology and size. Deep-bodied and laterally compressed striped blennies used longer shells with wider gapes as nesting sites while naked gobies that have a round body shape typically occupied shorter shells with narrower gapes (Crabtree and Middaugh 1982). Striped blennies, naked gobies, and other cryptic temperate demersal fishes (e.g., feather blenny, crested blenny, freckled blenny) coexist on oyster reefs because their habitat requirements do not completely overlap.

Small (< 100 mm SL) demersal fishes like gobies and blennies are adapted to the heterogeneous interstitial spaces within biogenic habitats (e.g., oyster reefs, coral reefs) that provide many small-scale (mm) ecological niches (Hutchinson 1959; Munday and Jones 1998; Pratt and Lauer 2013). Coral reef gobies partition heterogeneous coral habitats on the basis of body morphology and size (e.g., *Gobiodon histrio, G. rivulatus*, Gobiidae, Untersteggaber et al. 2014; Wehrberger and Herler 2014). The observed differences in temperate goby and blenny body morphologies and sizes suggest that these fishes rely on different small-scale (mm) heterogeneous oyster reef spaces.

Ontogenetic shifts in habitat use allow naked goby and striped blenny larvae, juveniles, and adults to realize different niches and reduce competition between their life stages. The morphological differences observed between newly settled naked goby and striped blenny larvae may reduce competition for habitat space once they become benthic. The body morphology of naked goby and striped blenny juveniles are similar to those of adults. Naked goby juveniles are more elongate and slender than striped blenny juveniles which are deep-bodied and robust (Hildebrand and Cable 1938). Juveniles of both species likely exhibit different predator avoidance and prey capture behavioral strategies than conspecific adults due to their smaller size. Ontogenetic shifts in habitat use were described for a species of tropical coral reef blenny *Acanthemblemaria crockery* which inhabits invertebrate tubes as an adult, but does not during its juvenile stage (Hastings and Galland 2010). It is likely that naked goby and striped blenny juveniles also exhibit ontogenetic shifts in habitat use by moving into larger shell spaces as they grow.

Naked gobies and striped blennies also display differences in larval period duration and growth rates that act to reduce overlap within the plankton as well as benthic settlement habitats. The shorter larval periods observed in striped blenny larvae reduce the time naked gobies and striped blennies occur together in the water column. Increased growth rates observed later in the spawning season resulted in shorter settlement lengths. Shorter settlement lengths allow late season newly settled larvae to use smaller shells or spaces than older, conspecific juveniles and may reduce competition for space between larval cohorts after settlement.

Adult reproductive biology sets the stage for the observed resource partitioning by temperate reef fishes. Water temperature changes may influence phenology including the timing of reproduction. Increased winter water temperatures (~1.8°C) observed in North Inlet estuary between 1979 and 2007 (Allen et al. 2008) may impact temperate reef fish annual gonadal development and spawning season cycles. Although day-length appeared to be an important factor determining the onset of naked goby and striped blenny spawning cycles, increases in water temperature may also impact annual fish reproductive cycles (Shoji et al. 2011). Species-specific naked goby and striped blenny responses to increasing winter water temperatures are unknown. However, temporal changes in the start of their spawning seasons could disrupt the observed temporal offset of larvae in the water column and subsequent early life history dynamics.

The trophic structure within temperate estuaries is facilitated by the observed spatial and temporal habitat partitioning between demersal fishes. Differences in the realized niche for naked gobies and striped blennies at all life history stages are likely mirrored by the other sympatric demersal fishes. The observed life history plasticity combined with the broad physiological tolerances of these generalist fishes has allowed them to be successful in estuarine habitats at evolutionary time scales. The success of these demersal fishes enhances upper level piscivore food resources in the plankton as well as on the benthos. The nesting behavior of adult male demersal fishes combined with the swimming and feeding behavior of benthic sub-adults helps remove sediment from the oyster shell surface facilitating oyster metamorphosis and recruitment, and, effectively, creation of their habitat. Spatial and temporal resource partitioning offers an effective strategy to promote success of naked gobies and striped blennies as well as the associated communities.

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VITA

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Appendix 1: Linear regression coefficients with (standard error) used to test the slopes between male and female naked goby and striped blenny standard length (SL, mm) and body depth (BD, mm), whole fish wet tissue weight (WTW, g) and whole fish dry tissue weight (DTW, g), and SL and whole fish WTW and whole fish DTW. The equation and model coefficients are described in the text. n equals the number of fish measured.

Species	Sex	Relationship	n	b		m		R^2
Naked goby	Male	SL:BD	17	0.29	(1.37)	0.15	(0.05)	0.43
		Whole fish WTW: whole fish DTW	85	0.02	(0.01)	0.20	(0.01)	0.91
		Log (SL): Log (whole fish WTW)	85	-4.42	(0.21)	2.80	(0.14)	0.84
		Log (SL) : Log (whole fish DTW)	85	-4.87	(0.19)	2.66	(0.12)	0.86
	Female	SL:BD	4	-0.33	(6.87)	0.17	(0.23)	0.20
		Whole fish WTW: whole fish DTW	14	0.01	(0.01)	0.23	(0.03)	0.87
		Log (SL): Log (whole fish WTW)	14	-5.24	(0.66)	3.30	(0.44)	0.82
		Log (SL) : Log (whole fish DTW)	14	-5.70	(0.52)	3.20	(0.35)	0.87
Striped blenny	Male	SL:BD	16	0.72	(1.01)	0.24	(0.02)	0.91
		Whole fish WTW: whole fish DTW	70	0.04	(0.02)	0.22	(0.01)	0.96
		Log (SL): Log (whole fish WTW)	70	-4.58	(0.20)	2.90	(0.12)	0.90
		Log (SL) : Log (whole fish DTW)	70	-5.11	(0.80	2.84	(0.10)	0.92
	Female	SL:BD	12	-4.26	(2.84)	0.36	(0.06)	0.77
		Whole fish WTW: whole fish DTW	42	0.01	(0.02)	0.23	(0.01)	0.94
		Log (SL): Log (whole fish WTW)	42	-4.42	(0.27)	2.82	(0.16)	0.88
		Log (SL) : Log (whole fish DTW)	42	-5.10	(0.24)	2.86	(0.15)	0.91

Appendix 2: Summary of t-tests performed to evaluate sex-specific differences between naked goby and striped blenny linear regression slopes. SL equals standard length (mm). WTW equals wet tissue weight (g). DTW equals dry tissue weight (g). Asterisks indicate significance at the alpha = 0.05 level.

Species	Relationship	n	df	t	p-value
Naked goby	SL : BD	21	17	0.40	>0.05
	Whole fish WTW : Whole fish DTW	99	95	1.97	>0.05
	Log (SL) : Log (whole fish WTW)	99	95	3.14	<0.05*
	Log (SL) : Log (whole fish DTW)	99	95	2.70	<0.05*
Striped blenny	SL : BD	28	24	0.90	>0.05
	Whole fish WTW : Whole fish DTW	112	108	1.11	>0.05
	Log (SL) : Log (whole fish WTW)	112	108	3.76	<0.05*
	Log (SL) : Log (whole fish DTW	112	108	3.86	<0.05*

Appendix 3: Naked goby and striped blenny week of the spawning season relative to calendar date on Sunday of each week during 2012 and average weekly water temperature (WT, °C, standard deviation). Water temperature data were recorded by an automated water monitoring station at Crabhaul Creek, North Inlet, SC (NERR CDMO; cdmo.baruch.sc.edu).

Week of the spawning season	Naked goby Date	Avg. WT (°C)	Striped blenny Date	Avg. WT (°C)
0	04/01/2012	20.9 (2.13)	03/11/2012	14.8 (2.72)
1	04/08/2012	20.8 (2.02)	03/18/2012	18.6 (2.26)
2	04/15/2012	19.4 (1.25)	03/25/2012	21.6 (2.57)
3	04/22/2012	21.7 (2.93)	04/01/2012	20.9 (2.13)
4	04/29/2012	21.1 (1.70)	04/08/2012	20.8 (2.02)
5	05/06/2012	25.2 (1.67)	04/15/2012	19.4 (1.25)
6	05/13/2012	24.1 (1.71)	04/22/2012	21.7 (2.93)
7	05/20/2012	23.6 (0.66)	04/29/2012	21.1 (1.70)
8	05/27/2012	25.3 (1.29)	05/06/2012	25.2 (1.67)
9	06/03/2012	27.3 (1.95)	05/13/2012	24.1 (1.71)
10	06/10/2012	25.2 (0.83)	05/20/2012	23.6 (0.66)
11	06/17/2012	26.1 (2.01)	05/27/2012	25.3 (1.29)
12	06/24/2012	27.9 (2.25)	06/03/2012	27.3 (1.95)
13	07/01/2012	27.3 (2.11)	06/10/2012	25.2 (0.83)
14	07/08/2012	30.1 (1.48)	06/17/2012	26.1 (2.01)
15	07/15/2012	29.7 (1.23)	06/24/2012	27.9 (2.25)
16	07/22/2012	30.0 (1.53)	07/01/2012	27.3 (2.11)
17	07/29/2012	30.1 (1.80)	07/08/2012	30.1 (1.48)
18	08/05/2012	28.8(1.53)	07/15/2012	29.7 (1.23)
19	08/12/2012	29.5 (1.13)	07/22/2012	30.0 (1.53)
20	08/19/2012	29.4 (1.24)	07/29/2012	30.1 (1.80)
21	08/26/2012	27.1 (1.38)	08/05/2012	28.8(1.53)
22			08/12/2012	29.5 (1.13)
23			08/19/2012	29.4 (1.24)
24			08/26/2012	27.1 (1.38)
25			09/02/2012	27.8 (1.34)
26			09/09/2012	29.7 (1.34)
27			09/16/2012	26.6 (1.57)
28			09/23/2012	26.6 (1.18)
29			09/30/2012	25.0 (1.44)

Appendix 4: Naked goby and striped blenny week of the spawning season relative to calendar date on Sunday of each week for 2013 and average weekly water temperature (WT, °C, standard deviation). Water temperature data were recorded by an automated water monitoring station at Crabhaul Creek, North Inlet, SC (NERR CDMO; cdmo.baruch.sc.edu).

	Naked goby		**Striped blenny**	
Week of the spawning season	Date	Avg. WT (°C)	Date	Avg. WT (°C)
0	04/14/2013	15.5 (2.13)	03/24/2013	12.5 (2.03)
1	04/21/2013	19.9 (3.01)	03/31/2013	15.5 (2.13)
2	04/28/2013	22.2 (2.47)	04/07/2013	19.9 (3.01)
3	05/05/2013	18.7 (2.38)	04/14/2013	22.2 (2.47)
4	05/12/2013	19.9 (1.80)	04/21/2013	18.7 (2.38)
5	05/19/2013	21.0 (2.60)	04/28/2013	19.9 (1.80)
6	05/26/2013	23.6 (2.45)	05/05/2013	21.0 (2.60)
7	06/02/2013	24.5 (1.77)	05/12/2013	23.6 (2.45)
8	06/09/2013	26.0 (2.68)	05/19/2013	24.5 (1.77)
9	06/16/2013	26.3 (1.11)	05/26/2013	26.0 (2.68)
10	06/23/2013	29.3 (2.18)	06/02/2013	26.3 (1.11)
11	06/30/2013	27.1 (1.35)	06/09/2013	29.3 (2.18)
12	07/07/2013	28.3 (1.64)	06/16/2013	27.1 (1.35)
13	07/14/2013	28.1 (1.43)	06/23/2013	28.3 (1.64)
14	07/21/2013	29.2 (1.81)	06/30/2013	28.1 (1.43)
15	07/28/2013	29.7 (1.31)	07/07/2013	29.2 (1.81)
16	08/4/2013	28.0 (1.85)	07/14/2013	29.7 (1.31)
17	08/11/2013	28.7 (0.88)	07/21/2013	28.0 (1.85)
18	08/18/2013	28.6 (1.58)	07/28/2013	28.7 (0.88)
19	08/25/2013	27.3 (3.15)	08/04/2013	28.6 (1.58)
20	09/01/2013	28.2 (1.93)	08/11/2013	27.3 (3.15)
21	09/08/2013	27.5 (1.47)	08/18/2013	28.2 (1.93)
22			08/25/2013	27.5 (1.47)
23			09/01/2013	29.3 (1.06)
24			09/08/2013	28.5 (1.31)
25			09/15/2013	26.2 (1.47)
26			09/22/2013	24.2 (1.37)
27			09/29/2013	23.8 (1.57)
28			10/06/2013	22.8 (0.89)
29			10/13/2013	19.7 (2.44)

Appendix 5: Demographic description of male naked gobies collected from North Inlet, SC from June 2012 through December 2013. CumWOY indicates cumulative week of the years; WOS indicates week of the spawning season.

		Standard length (mm)										
CumWOY	WOS	15.0-19.9	20.0-2.94	25.0-29.9	30.0-34.9	35.0-39.9	40.0-44.9	45.0-49.9	50.0-54.9	55.0-59.9	60.0-64.9	65.0-69.9
23	10	0	0	0	0	0	2	3	0	0	0	0
28	15	0	2	2		5	0	1	0	0	0	0
31	18	0		1	3	2	1	0	0	0	0	0
37	-	0	0	0	0	0	0	0	0	0	0	0
42	-	0	0	0	0	0	0	0	0	0	0	0
46	-	0	0	0	0	0	0	0	0	0	0	0
50	-	0	0	0	0	0	0	0	0	0	0	0
55	-	0	0	0	0	0	0	0	0	0	0	0
60	-	0	0	1	0	0	0	0	0	0	0	0
64	-	0	1	0	0	0	0	0	0	0	0	0
68	1	0	2	3	1	0	0	3	2	1	0	0
72	5	0	0	0	0	0	4	4	3	0	0	0
77	10	0	0	0	0	0	5	6	0	0	0	0
80	13	0	0	0	0	3	2	2	0	0	0	0
85	18	0	0	0	0	1	1	0	0	0	0	0
89	-	0	0	0	0	0	0	0	0	0	0	0
93	-	0	1	0	1	1	0	0	0	0	0	0
97	-	0	1	2	2	0	0	0	0	0	0	0
100	-	0	0	4	3	2	0	0	0	0	0	0

Appendix 6: Demographic description of female naked gobies collected from North Inlet, SC from June 2012 through December 2013. CumWOY indicates cumulative week of the years; WOS indicates week of the spawning season.

		Standard length (mm)										
CumWOY	WOS	15.0-19.9	20.0-2.94	25.0-29.9	30.0-34.9	35.0-39.9	40.0-44.9	45.0-49.9	50.0-54.9	55.0-59.9	60.0-64.9	65.0-69.9
23	10	0	0	0	0	0	1	0	0	0	0	0
28	15	0	0	1	0	1	0	0	0	0	0	0
31	18	0	0	0	0	0	0	0	0	0	0	0
37	-	0	0	0	0	0	0	0	0	0	0	0
42	-	0	0	0	0	0	0	0	0	0	0	0
46	-	0	0	0	0	0	0	0	0	0	0	0
50	-	0	0	0	0	0	0	0	0	0	0	0
55	-	0	0	0	0	0	0	0	0	0	0	0
60	-	0	1	0	1	0	0	0	0	0	0	0
64	-	0	1	0	0	0	0	0	0	0	0	0
68	-	0	0	0	1	0	0	0	0	0	0	0
72	5	0	0	0	0	1	0	0	0	0	0	0
77	10	0	0	0	0	1	0	0	0	0	0	0
80	13	0	0	0	0	1	0	0	0	0	0	0
85	18	0	0	0	0	0	0	0	0	0	0	0
89	-	0	0	0	0	0	0	0	0	0	0	0
93	-	0	0	1	1	0	0	0	0	0	0	0
97	-	0	0	1	0	0	0	0	0	0	0	0
100	-	0	0	0	1	0	0	0	0	0	0	0

Appendix 7: Demographic description of indeterminate naked gobies collected from North Inlet, SC from June 2012 through December 2013. CumWOY indicates cumulative week of the years; WOS indicates week of the spawning season.

		Standard length (mm)										
CumWOY	WOS	15.0-19.9	20.0-2.94	25.0-29.9	30.0-34.9	35.0-39.9	40.0-44.9	45.0-49.9	50.0-54.9	55.0-59.9	60.0-64.9	65.0-69.9
23	10	0	0	1	0	0	0	0	0	0	0	0
28	15	0	0	1	0	1	0	0	0	0	0	0
31	18	0	0	1	2	0	0	0	0	0	0	0
37	-	0	0	0	0	0	0	0	0	0	0	0
42	-	0	2	0	0	0	0	0	0	0	0	0
46	-	0	0	0	0	0	0	0	0	0	0	0
50	-	0	0	0	0	0	0	0	0	0	0	0
55	-	0	0	1	0	0	0	0	0	0	0	0
60	-	1	2	0	0	0	0	0	0	0	0	0
64	-	0	3	1	0	0	0	0	0	0	0	0
68	-	0	0	0	0	0	0	0	0	0	0	0
72	5	0	0	0	0	0	0	0	0	0	0	0
77	10	0	0	0	0	0	0	0	0	0	0	0
80	13	0	0	0	0	0	0	0	0	0	0	0
85	18	0	0	0	0	0	0	0	0	0	0	0
89	-	0	0	0	0	0	0	0	0	0	0	0
93	-	0	1	0	0	0	0	0	0	0	0	0
97	-	0	0	0	0	0	0	0	0	0	0	0
100	-	0	2	0	0	0	0	0	0	0	0	0

Appendix 8: Demographic description of male striped blennies collected from North Inlet, SC from June 2012 through December 2013. CumWOY indicates cumulative week of the years; WOS indicates week of the spawning season.

		Standard length (mm)										
CumWOY	WOS	15.0-19.9	20.0-2.94	25.0-29.9	30.0-34.9	35.0-39.9	40.0-44.9	45.0-49.9	50.0-54.9	55.0-59.9	60.0-64.9	65.0-69.9
31	21	0	0	0	0	1	3	1	3	1	1	0
37	27	0	0	0	0	0	0	1	0	1	0	0
42	-	0	0	0	0	0	1	0	1	3	0	0
46	-	0	0	0	0	0	0	0	0	0	0	0
50	-	0	0	0	0	0	0	0	0	0	0	0
55	-	0	0	0	0	0	0	0	1	0	0	0
60	-	0	0	0	0	0	0	0	5	0	0	0
64	0	0	0	0	0	0	0	0	2	0	0	0
68	4	0	0	0	0	0	0	0	1	1	3	0
72	8	0	0	0	0	0	0	0	2	2	1	0
77	13	0	0	0	0	0	0	1	1	2	2	1
80	16	0	0	0	0	0	0	0	2	3	3	0
85	21	0	0	0	0	0	2	0	0	2	2	0
89	25	0	0	0	1	0	0	0	0	0	3	0
93	29	0	0	0	0	1	1	0	1	0	0	1
97	-	0	0	2	0	0	0	0	0	2	0	0
100	-	0	0	1	1	1	0	0	0	0	1	0

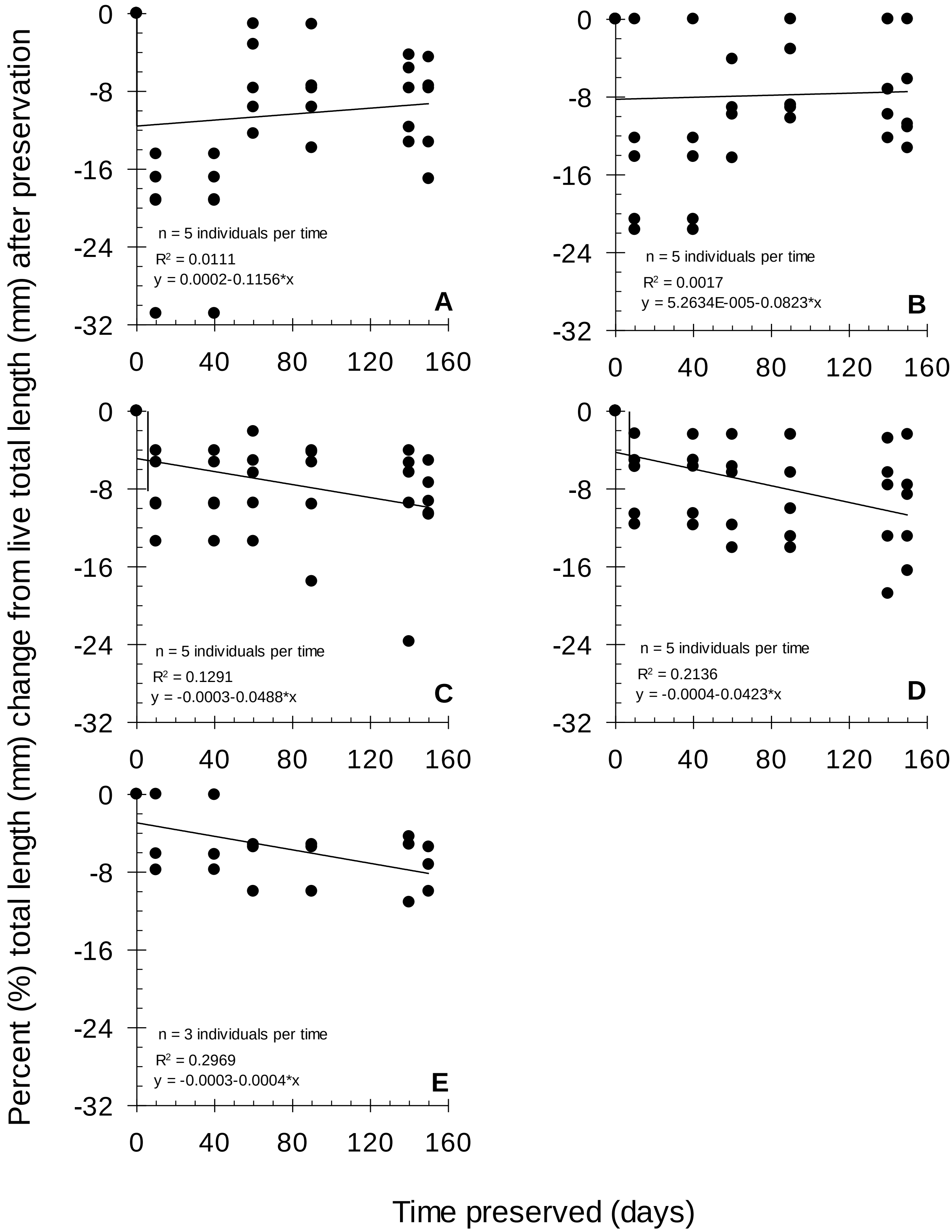
Appendix 9: Demographic description of female striped blennies collected from North Inlet, SC from June 2012 through December 2013. CumWOY indicates cumulative week of the years; WOS indicates week of the spawning season.

		Standard length (mm)										
CumWOY	WOS	15.0-19.9	20.0-2.94	25.0-29.9	30.0-34.9	35.0-39.9	40.0-44.9	45.0-49.9	50.0-54.9	55.0-59.9	60.0-64.9	65.0-69.9
31	21	0	0	0	1	1	0	1	0	0	0	0
37	27	0	0	0	0	0	0	1	0	0	0	0
42	-	0	0	1	0	1	0	4	1	1	0	0
46	-	0	0	0	0	0	0	0	0	0	0	0
50	-	0	0	0	0	0	0	0	0	0	0	0
55	-	0	0	0	0	0	0	0	0	0	0	0
60	-	0	0	2	2	2	0	1	0	0	0	0
64	0	0	0	0	0	0	0	0	0	0	0	0
68	4	0	0	0	0	0	1	0	0	0	0	0
72	8	0	0	0	0	0	0	0	1	1	0	0
77	13	0	0	0	0	0	0	1	0	0	0	0
80	16	0	0	0	0	0	0	0	2	1	0	0
85	21	0	0	0	0	0	4	0	0	0	0	0
89	25	0	0	0	0	0	0	0	0	0	0	0
93	29	0	0	0	1	0	1	1	1	1	0	0
97	-	0	0	0	0	0	0	0	0	0	0	0
100	-	0	0	0	0	0	0	0	0	0	0	0

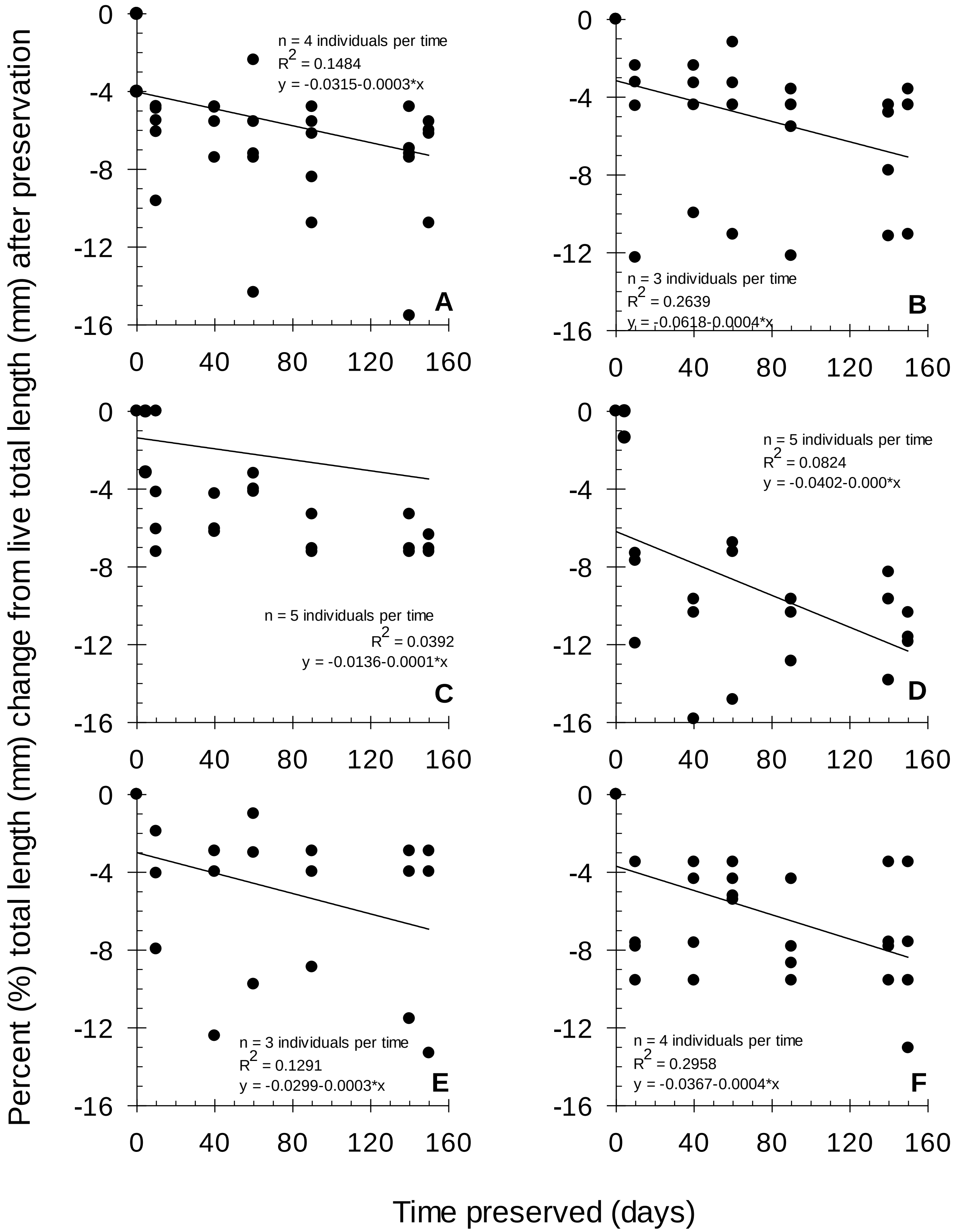
Appendix 10: Demographic description of indeterminate striped blennies collected from North Inlet, SC from June 2012 through December 2013. CumWOY indicates cumulative week of the years; WOS indicates week of the spawning season.

		Standard length (mm)										
CumWOY	WOS	15.0-19.9	20.0-2.94	25.0-29.9	30.0-34.9	35.0-39.9	40.0-44.9	45.0-49.9	50.0-54.9	55.0-59.9	60.0-64.9	65.0-69.9
31	21	0	0	0	0	0	0	0	0	0	0	0
37	27	0	0	0	0	0	0	0	0	0	0	0
42	-	0	0	0	0	0	0	0	0	0	0	0
46	-	0	0	0	0	0	0	0	0	0	0	0
50	-	0	0	0	0	0	0	0	0	0	0	0
55	-	0	0	0	0	0	0	0	0	0	0	0
60	-	0	0	0	0	0	0	0	0	0	0	0
64	0	0	0	0	0	0	0	0	0	0	0	0
68	4	0	0	0	0	0	0	0	0	0	0	0
72	8	0	0	0	0	0	0	0	0	0	0	0
77	13	0	0	0	0	0	0	0	0	0	0	0
80	16	0	0	0	0	0	0	0	0	0	0	0
85	21	0	1	0	0	0	0	0	0	0	0	0
89	25	0	0	0	0	0	0	0	0	0	0	0
93	29	0	0	0	0	0	0	0	0	0	0	0
97	-	0	0	2	1	0	0	0	0	0	0	0
100	-	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: Percent (%) total length (mm) change from live total length (mm) for (A) age 0, (B) age 3, (C) age 6, (D) age 9 and (E) age 15 dph naked goby larvae after preservation in 10% Borax buffered formalin.


Percent (%) total length (mm) change from live total length (mm) after preservation
Time preserved (days)
n = 5 individuals per time
R² = 0.0111
y = 0.0002-0.1156*x
A
n = 5 individuals per time
R² = 0.0017
y = 5.2634E-005-0.0823*x
B
n = 5 individuals per time
R² = 0.1291
y = -0.0003-0.0488*x
C
n = 5 individuals per time
R² = 0.2136
y = -0.0004-0.0423*x
D
n = 3 individuals per time
R² = 0.2969
y = -0.0003-0.0004*x
E

Appendix 12: Percent (%) total length (mm) change from live total length (mm) for (A) age 0, (B) age 3, (C) age 6, (D) age 9, (E) age 12 and (F) age 19 dph striped blenny larvae after preservation in 10% Borax buffered formalin.



Percent (%) total length (mm) change from live total length (mm) after preservation
Time preserved (days)
n = 4 individuals per time
R2 = 0.1484
y = -0.0315-0.0003*x
A
n = 3 individuals per time
R2 = 0.2639
y = -0.0618-0.0004*x
B
n = 5 individuals per time
R2 = 0.0392
y = -0.0136-0.0001*x
C
n = 5 individuals per time
R2 = 0.0824
y = -0.0402-0.000*x
D
n = 3 individuals per time
R2 = 0.1291
y = -0.0299-0.0003*x
E
n = 4 individuals per time
R2 = 0.2958
y = -0.0367-0.0004*x
F