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Age, growth, and long-distance dispersal in the western North Atlantic of vexillifer larvae of the pearlfish, *Echiodon dawsoni*, with notes on *Carapus bermudensis* (Ophidiiformes: Carapidae)

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Abstract We examined 120 vexillifer larvae of *Echiodon dawsoni* and 40 of *Carapus bermudensis* collected from the continental shelf and slope of the Gulf of Mexico and the western North Atlantic to Nova Scotia. Age was estimated for a subset of vexillifers, from which otoliths (sagittae) were excised and growth increments were recognizable, and a linear, estimated age at length relation was constructed. Spawning appeared to be year round for both species across their range. All estimated age classes of *Ec. dawsoni* were collected south of 35 °N, but north of 35 °N all vexillifers of *Ec. dawsoni* were older than 55 days. Only one *C. bermudensis* was collected north of 35 °N. The occurrence of vexillifers of *Ec. dawsoni* north of Cape Hatteras, North Carolina, USA, indicates long-distance dispersal to inhospitable habitats and might be related to their spawning farther offshore than *C. bermudensis*, in regions where their vexillifers are more likely to be entrained into the Gulf Stream and transported northeastward.

Keywords *Echiodon dawsoni* · *Carapus bermudensis* · Vexillifers · Growth · Dispersal

Introduction

The pearlfish family Carapidae, with highly specialized larvae, multiple growth stages, and inquilinous commensalism of some adults, is exceptional among fishes (Parmentier and Vandewalle 2003). All carapids possess specialized vexillifer larvae, a definitive family feature (Markle and Olney 1990), characterized by an elongate, filamentous, and ornamented dorsal fin ray, the vexillum (Govoni et al. 1984). Other larval specializations include ornamented caudal fin extensions and exterilium guts (Markle and Olney 1990; Fahay and Nielsen 2003).

Most carapids exhibit four stages that correspond generally to habitats and growth: (1) a planktonic vexillifer, when head length (HL) and total length (TL) increase; (2) usually a benthic-pelagic transitional tenuis, when TL decreases precipitously and larvae settle to benthic habitats; (3) a benthic, free-living or inquiline juvenile, when TL increases; and (4) a benthic, free-living or inquiline adult, when body depth and TL increase (Gordon et al. 1984; Parmentier et al. 2002a, Parmentier et al. 2002b, Parmentier et al. 2004a). The decreasing TL of tenuis larvae is peculiar, but shared with some other fishes such as Elopomorpha (Parmentier et al. 2004a). Adult carapids are more peculiar in habit: *Carapus*, *Encheliophis*, and *Onuxodon* are inquilines in a variety of invertebrates (Markle and Olney 1990; Tyler et al. 1992; Parmentier et al. 2000), and *Encheliophis* parasitize their hosts (Parmentier et al. 2010). Pyramodontines, *Eurypleuron*, and *Echiodon* are reportedly free living as adults (Markle and Olney 1990; Olney 2006).

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Information on the duration of early life history stages of carapids is sparse and restricted to Carapini. At settlement the larvae of *Carapus boraborensis* and *Carapus homei* had mean sagittal increment counts of 48 (± 6) and 83 (± 5), whereas *Encheliophis gracilis* had a mean of 68 (± 7) (Parmentier et al. 2002a, Parmentier et al. 2002b). A *Carapus bermudensis* tenuis larva had 85 increments to the apparent transition, the first discontinuity in spacing of otolith increments (Smith et al. 1981). Larvae of the Carapini, therefore, appear to remain pelagic for extended periods with indications of plasticity in the duration of the vexillifer and tenuis stages (Colley et al. 2008). Vexillifers of *C. homei* can delay vexillifer to tenuis transition for 21 days (d) depending on oceanographic conditions (Parmentier et al. 2004b). Despite specific and restricted adult habitats, most carapid species are wide ranging, because of their teleplanktonic larvae (Markle and Olney 1990); *Echiodon dawsoni*, for example, has been reported as far north as Nova Scotia (Markle et al. 1980).

In the western Atlantic, pelagic vexillifers of three species, *Ec. dawsoni*, *C. bermudensis*, and *Snyderidia canina*, have been collected (Olney and Markle 1979; Olney 2006; Namiki et al. 2007). Here, we describe the growth of the vexillifers of *Ec. dawsoni* and *C. bermudensis*, describe distribution patterns, and infer the effects of Gulf Stream dispersal.

Material and methods

Collections. Data for all available collections of carapid larvae from the western North Atlantic were obtained from the United States National Museum (USNM), from the Scotian Shelf (off Nova Scotia, Canada) Ichthyoplankton Program (SSIP), and from collections taken on regional cruises in the northern Gulf of Mexico and off the southeastern coast of the United States (U. S.). The Gulf of Mexico (GOMEX) collections (Sogard et al. 1987; Govoni et al. 1989; Govoni and Grimes 1992; Govoni 1993) were taken from 23 cruises between 1979 and 2000, and consisted of approximately 1,833 collections. The number of cruises by season was: December–February (10), March–May (5), June–August (3), and September–November (5) (Govoni, unpublished). The southeastern U. S. (SAB) collections were taken between 1979 and 2003 (Govoni 1993; Govoni and Pietrafesa 1994; Govoni and Spach 1999; Powell et al. 2000; Hare and Govoni 2005; Quattrini et al. 2005; Govoni et al. 2010, Govoni et al. 2013). Collecting was year round, but the greatest effort was in December–February (Govoni, unpublished). Most of the SSIP collections were taken from 34 cruises between 1976 and 1982 and consisted of 3,927 collections (Markle et al. 1980; Hanke et al. 2000). The number of cruises by season

was: December–February (5), March–May (7), June–August (13), and September–November (9) (Hanke et al. 2000). Collections were made with a variety of gears: 60 cm diameter bongo nets; a 1 m MOCNESS (Wiebe et al. 1976); a Tucker Trawl (Davies and Barham 1969); and a BFN-1 net (Tareq and Co., Miami). Temperature (T) and salinity (S) data were available from selected collections. The SSIP collections were fixed in 5 % formalin, while the GOMEX and SAB collections were preserved in 99 % (volume) ethanol and used for age estimation. One *Snyderidia canina* was in the collections, but excluded from analysis.

Otoliths. Otoliths were excised from specimens collected from the regional cruises, GOMEX, and SAB. Head length (HL) was measured to the nearest 0.01 mm with an ocular micrometer following Markle and Olney (1990) and total length (TL) to the nearest 0.1 mm made when possible. Otoliths were removed by using the teasing method described in Secor et al. (1992) with cross-polarized light and affixed to glass slides using Crystal Bond thermoplastic resin. Sagitta from small larvae required no further preparation before analyzing; sagittae from large larvae were carefully sanded using 2,000 grit wet/dry sandpaper to a plane near the core and polished on a felt pad using 0.05 μm alumina powder. Sagittae were found in 28 of 60 *Echiodon dawsoni* and 15 of 20 *Carapus bermudensis*; lapilli were found in some of each species.

Growth increments were counted on both sagittae. Bilateral sagittae were analyzed three times using a compound microscope under a 50x oil immersion objective. An image analysis system equipped with a Leica DFC320 camera and Leica Application Suite software enlarged images of sagittae so that counts of growth increments could be made. The median increment count was assigned to each sagitta. The greater increment count of the two sagittae was used in all analyses.

All sagittae from larvae collected before 1993 were analyzed by one person; those collected in 1993 and after were analyzed by another. Inasmuch as *Ec. dawsoni* was collected before and after 1993 and were analyzed by different people, ANCOVA tested for differences between regressions of HL on increment count. No significant differences between slopes ($P = 0.39$) or intercepts ($P = 0.16$) allowed the pooling of increment counts. The maximum diameter of sagittae was measured to the nearest 0.001 mm with an ocular micrometer along the long axis before otoliths were mounted by the first person following Parmentier et al. (2002a), and the longer diameter used for regression of maximum sagitta length and HL.

Growth. Regression was used to derive the best empirical fit for increment counts and HL. Linear, power, exponential, quadratic, and logistic models were used.

Criteria for best fit were: the regression coefficient, R^2 ; dispersion or convergence of residuals; and graphical display with the most biologically realistic parameter estimates, following Govoni et al. (2003). We assumed one increment was deposited each day after hatching (Campana 2001; Jones 2002) and used the selected model to assign ages to all vexillifers with a measured HL. Estimated ages were assigned from the regression estimate, adjusted for random error using a normal probability distribution of the standard error of the estimate.

Spawning. *Echiodon* and *Carapus* spawn buoyant eggs in mucilaginous masses (Emery 1880). Age from fertilization (AFF) was the estimated age of larvae plus an estimate of incubation time following Govoni et al. (2003): 3 d for *Echiodon* [based on Padoa (1956) for *Echiodon drummondii*] and 1 d for *C. bermudensis* (based on Padoa 1947 for *Carapus acus*). Estimated AFF was subtracted from the date of collection (DOY) to hind-cast the approximate spawning dates.

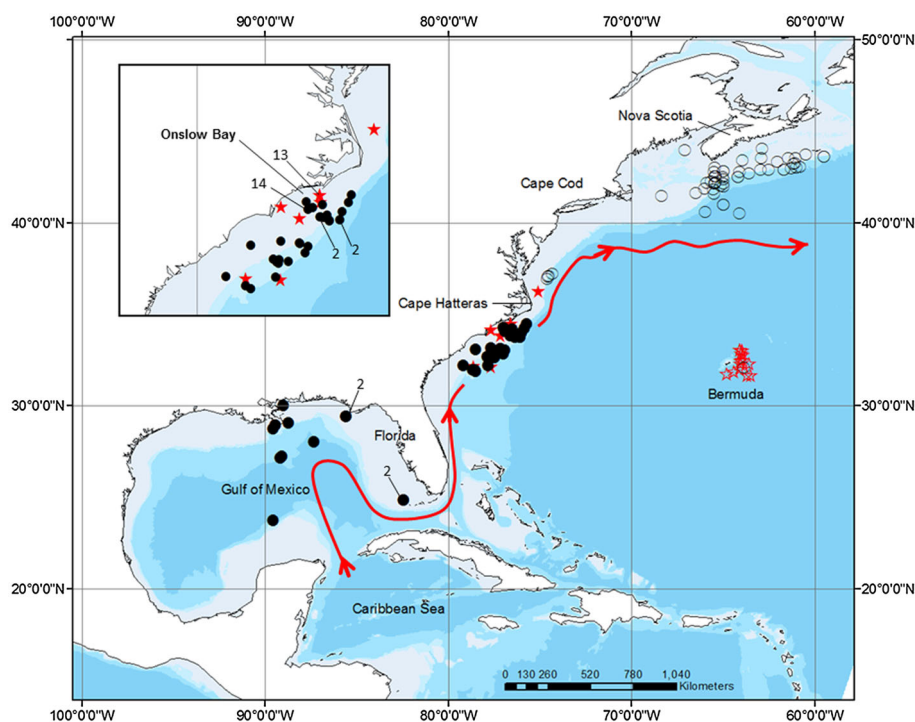
Retention and dispersal. We examined regional patterns of spawning dates and AFF to infer patterns of retention and dispersal. Regions with multiple AFF represented regions with potential recruitment, either retention or immigration, whereas regions with only older larvae could be used to estimate potential dispersal distances given known oceanic circulation in the northern Gulf of Mexico and the western North Atlantic.

Results

Collections. One hundred and twenty vexillifers of *Echiodon dawsoni* and 40 of *Carapus bermudensis* collected from the continental shelf and slope of the Gulf of Mexico and the western North Atlantic (Fig. 1) were examined. No yolk-sac vexillifers or tenuis larvae of any species were collected [one specimen of *C. bermudensis*, 4.83 mm HL, 140.0 mm TL, appeared to have a vexillum broken off and had an HL:TL ratio that was closer to that of a vexillifer (Markle and Olney 1990)]. In the GOMEX and SAB collections, seawater temperatures and salinities ranged 18.0–28.8 °C and 32.0–36.7 psu for *Ec. dawsoni* and 19.5–23.2 °C and 36.2 psu for *C. bermudensis*. One collection of *Ec. dawsoni* (1.68 mm HL; 20.0 mm TL) was taken with a MOCNESS at a discrete depth interval near the bottom; the net contained sand and shell fragments indicating that vexillifers of *Ec. dawsoni* occupy near-bottom habitats. Another *Ec. dawsoni* vexillifer, held alive shipboard after collection, was observed swimming in sigmoidal-wave action with a head-down posture.

Otolith morphology and microstructure. Sagittae of 28 pairs of otoliths of *Ec. dawsoni* were shaped as oblate spheroids, flattened longitudinally (Fig. 2a, b). No sulcus, rostrum, or post-rostrum (Parmentier et al. 2002a) was evident. The core was positioned to one side longitudinally. There were three checks, discontinuities in light refraction

Fig. 1 Collection localities of the vexillifer larvae of *Echiodon dawsoni* (circles) and *Carapus bermudensis* (stars) in the western North Atlantic [inset is a magnification of 30 to 40 °N latitude and 75 to 85 °W longitude; closed symbols depict localities for regional cruises and open symbols localities for USNM and SSIP collections; the arrow is an idealized representation of the trajectories of the Gulf Loop Current in the Gulf of Mexico and the Gulf Stream in the western North Atlantic taken from Murphy and Hurlburt (1999) and Hare et al. (2002); numbers indicate the collection of multiple specimens at a single location]



and radial spacing of increments, in *Ec. dawsoni* (Fig. 2c, d, e, f). The first check consisted of tightly spaced increments between the 5th and the 12th increments that followed evenly spaced increments from the core. On several sagittae, a second check was seen around the 19th increment and a third check between the 28th and the 32nd increments.

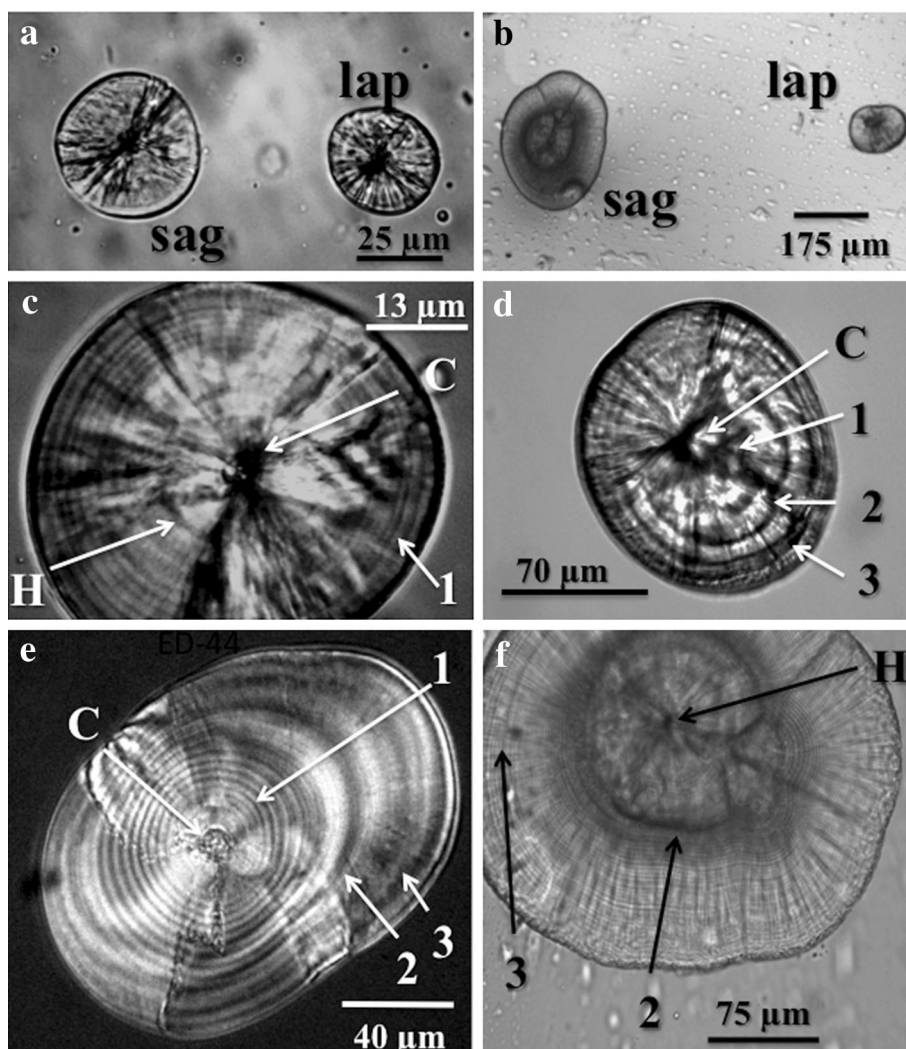
Sagittae of 15 *C. bermudensis* were also shaped as oblate spheroids, flattened longitudinally, but were more tapered than sagittae of *Ec. dawsoni* (Fig. 3a, b). No sulcus, rostrum, or post rostrum was evident, but a sagitta of a 4.83 mm HL, 140.0 mm TL vexillifer showed evidence of a post-rostral rim (Parmentier et al. 2001, 2007) (Fig. 3c). Increments 1–6 were evenly spaced; increments 7–13 were tightly spaced and constituted the first check (Fig. 3d). One larger vexillifer had checks at the 30th (the 2nd check) and the 60th (the 3rd check) increments.

Otolith microstructure and size of vexillifers. Head length of vexillifers increased linearly with TL for *Ec.*

dawsoni ($R^2 = 0.9536$) and *C. bermudensis* ($R^2 = 0.9564$) (Fig. 4). The youngest *Ec. dawsoni* had an HL of 0.83 mm, TL of 8.4 mm, and five increments, and the oldest was 4.33 mm HL, 63.0 mm TL, with 92 increments. The TL and HL of the largest *Ec. dawsoni* were approximately 65 % of the TL and HL of the largest vexillifer reported by Markle and Olney (1990). The youngest *C. bermudensis* was 0.46 mm in HL and 2.7 mm in TL, with one increment, and the oldest was 4.83 mm in HL and 140.0 mm in TL, with 77 increments. The TL and HL of the largest *C. bermudensis* were approximately 90 % of the TL and HL of the largest vexillifer reported by Markle and Olney (1990). The maximum diameter of sagittae was linearly related to head length for *Ec. dawsoni* ($R^2 = 0.8660$) (Fig. 5), and although data were limited, for *C. bermudensis* as well. Lapilli were smaller than sagittae (Figs. 2a, 3a).

Growth. We chose the linear model (Table 1), because head length was linearly related to increment number for

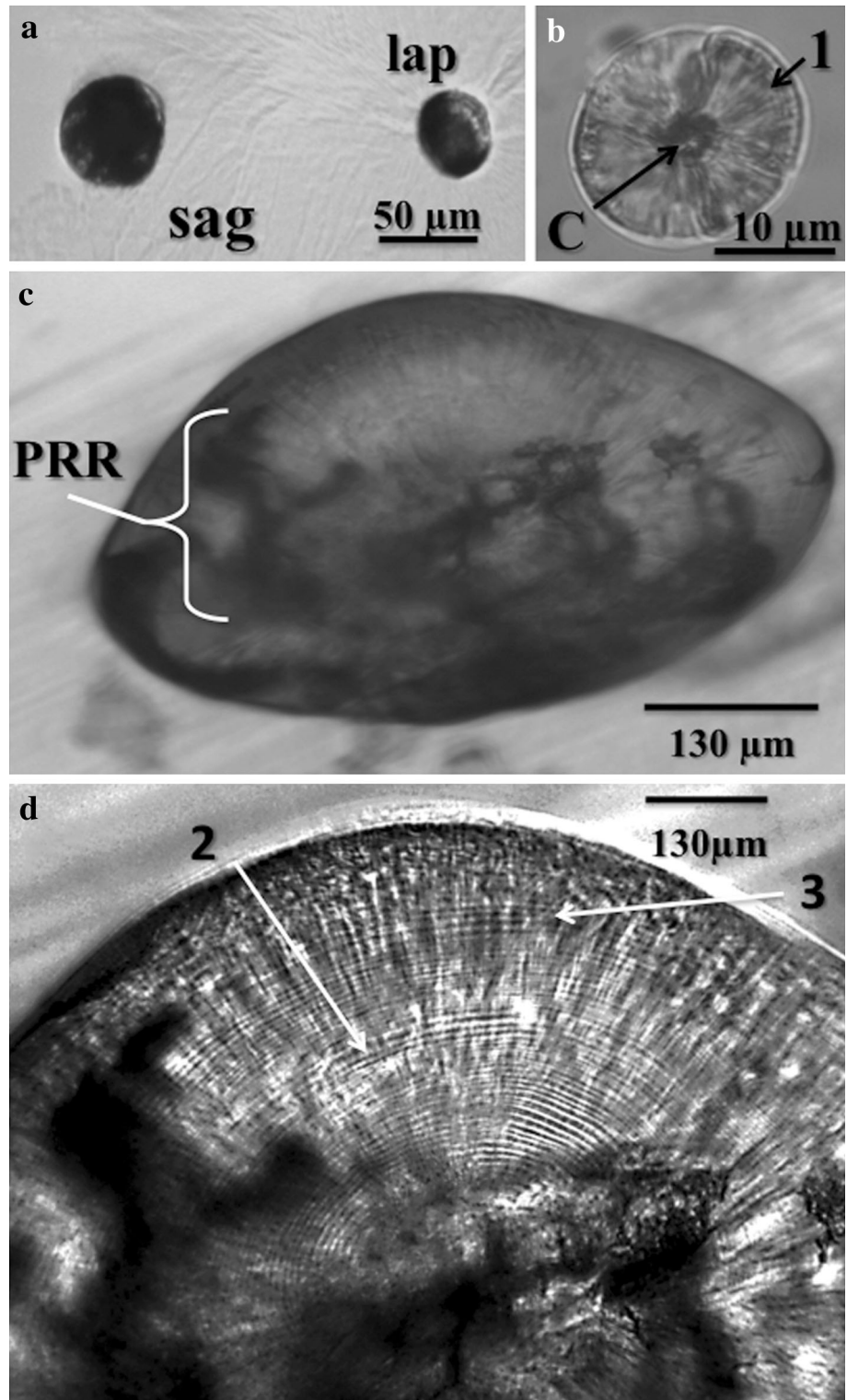
Fig. 2 Otoliths of the vexillifer larvae of *Echiodon dawsoni* collected from the western North Atlantic: **a** sagitta and lapillus from a 0.83 mm head length (HL) vexillifer; **b** sagitta and lapillus from a 3.1 mm HL vexillifer; **c** sagitta from a 0.88 mm HL vexillifer; **d** sagitta from a 3.10 mm HL vexillifer; **e** sagitta from a 1.80 mm HL vexillifer (interference contrast); **f** sagitta from a 3.10 mm HL vexillifer (C indicates the core; H the hatch mark at the first increment; numbers checks)



both *Ec. dawsoni* and *C. bermudensis* (Fig. 6a, b), and residuals were normally distributed. The R^2 for the linear model for *Ec. dawsoni* was 0.88, compared to 0.89 and 0.90 for the quadratic and power models, but the latter residuals were funnel shaped and inconstant. Other models

had lower R^2 . The R^2 for the linear model for *C. bermudensis* was 0.97, as was the R^2 for the quadratic model, but the latter failed the constant variance test ($P = 0.01$). Other models had lower R^2 . The regression models suggest that *Ec. dawsoni* had a larger HL at first increment formation

Fig. 3 Otoliths of the vexillifer larvae of *Carapus bermudensis* collected from the western North Atlantic: **a** sagitta and lapillus from a 1.88 mm head length (HL) vexillifer; **b** sagitta from a 0.62 mm HL vexillifer; **c** sagitta from a 4.83 mm HL vexillifer; **d** sagitta from the same vexillifer as (c) (*C* indicates the core; *PRR* post-rostral rim; *numbers* checks)



than *C. bermudensis*, but a slower growth rate (Fig. 6). A plot of total length against head length in *Ec. dawsoni* showed no decline in total length at larger head lengths as would be expected in a tenuis larva (Markle and Olney 1990). Data for *C. bermudensis* also showed no evidence of tenuis larvae, but data were sparse.

Spawning. The estimated back-calculated spawning months for *Ec. dawsoni* included every month, and there was a pronounced geographic pattern with those collected north of 35 °N, mostly having May to September as spawning months, and those south of 35 °N, mostly having December and January as spawning months (Fig. 7a). Scotian Shelf collections (north of 35 °N) covered all seasons, but there was heavier collecting effort in summer (38 % of cruises). Similarly, the GOMEX and the collections south of 35 °N covered all seasons, but there were more cruises in winter. There was also a difference in catch rates. North of 35 °N, all 55 collections of *Ec. dawsoni* were single specimen collections, whereas south of 35 °N, 9 of 22 (41 %) were multiple specimen collections with an average catch of 2.9 *Ec. dawsoni* per collection where at least one vexillifer was present.

All age classes (estimated 0–96 d) of *Ec. dawsoni* were collected south of 35 °N, while only older larvae (55–101 d) were collected north of 35 °N (Fig. 7b). Fourteen vexillifers of *Ec. dawsoni* (< 1 mm HL and < 5d AFF) were collected at a single location over a deep-water reef on the outer shelf in Onslow Bay (Fig. 1), just south of Cape Hatteras (Fig. 1) in January 1989 and January 2000. These collections also had vexillifers as large as 2.83 mm HL and 53 d AFF.

The estimated back-calculated spawning months for *C. bermudensis* included eight months and, although data were sparse, spawning is also likely year round. All but one *C. bermudensis* were collected south of 35 °N and they had estimated ages of 2–87 d. Most of the young vexillifers of *C. bermudensis* (Fig. 8) were collected over a reef at mid-shelf in Onslow Bay (Fig. 2) on two consecutive days in August 1991; these vexillifers were adrift for < 11 d.

Discussion

Whereas the duration of the vexillifer stages of *Echiodon dawsoni* and *Carapus bermudensis* was not determined, the sagittal otoliths of vexillifers indicated that growth was linear during the vexillifer stage, and estimated AFF, along with prevailing oceanic currents, explains the distribution of vexillifers. Sagittae of vexillifers of both species increased in diameter through the vexillifer stage, and there was no evidence that collections included transitional or tenuis stages that would be in the process of settlement. Markle and Olney (1990) inferred that *Ec. dawsoni* either

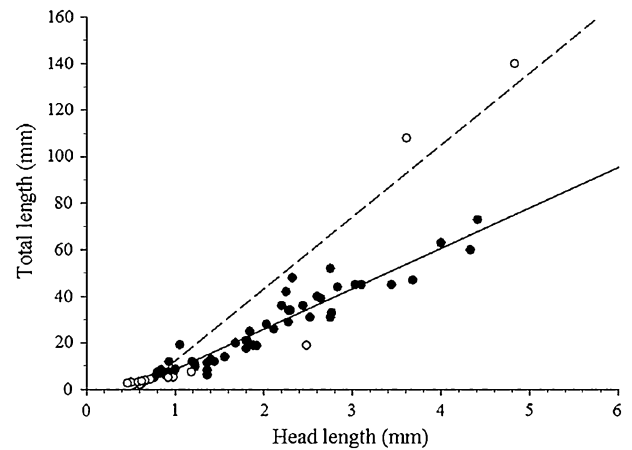


Fig. 4 Relation between total length and head length of vexillifer larvae collected from the western North Atlantic (*Echiodon dawsoni*, closed symbols and solid line; *Carapus bermudensis*, open symbols and dashed line)

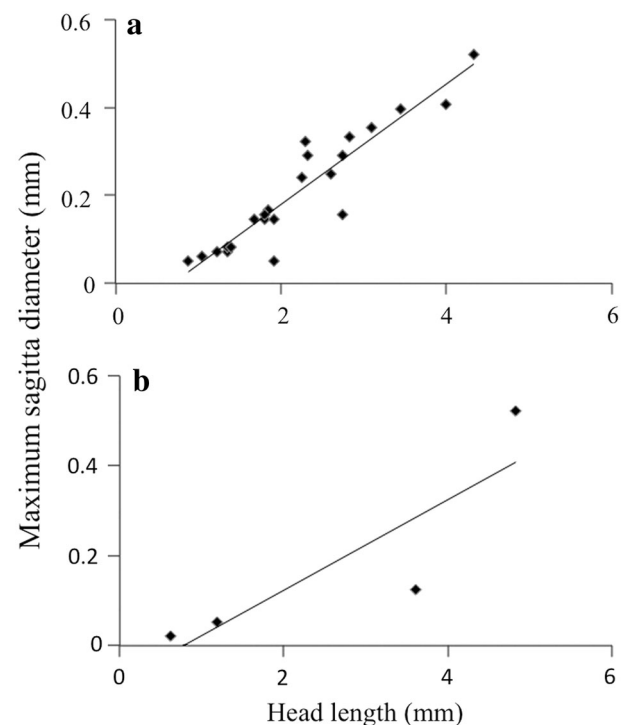


Fig. 5 Relation between the maximum sagittal length and head length of the vexillifer larvae of *Echiodon dawsoni* (a) and *Carapus bermudensis* (b)

lacks tenuis larvae or has a temporally abbreviated tenuis stage, while *C. bermudensis* is known to have a tenuis stage.

A check, from uniform to tightly spaced increments, typically marks the completion of yolk absorption and the beginning of exogenous feeding (Jones 2002). Although we found no vexillifers with yolk sacs or oil globules, the first check was between increments 5 and 12, 7 mm TL. This is

Table 1 Summary of models evaluated for describing growth of the vexillifer larvae of *Echiodon dawsoni* and *Carapus bermudensis*

| Genus species | Model | Model parameters | | | Model fit | | |
|----------------------------|--|------------------|--------|---------|-----------|-------------------------|---------------|
| | | y^0 | a | b | R^2 | Constant Variance Test | Residuals |
| <i>Echiodon dawsoni</i> | | | | | | | |
| | (1) $HL = y_0 + a \cdot IC$ | 0.8452 | 0.0393 | NA | 0.8794** | passed ($P = 0.7161$) | normal |
| | (2) $HL = a \cdot IC^b$ | NA | 0.3078 | 0.5747 | 0.8979** | passed ($P = 0.1909$) | funnel shaped |
| | (3) $HL = \exp^a \cdot IC$ | NA | 0.0175 | NA | 0.7644 | failed ($P = 0.0217$) | funnel shaped |
| | (4) $HL = y_0 + a \cdot IC + b \cdot IC^2$ | 0.6497 | 0.0542 | -0.0002 | 0.8904** | passed ($P = 0.4494$) | normal |
| | (5) $HL = a \cdot \ln IC - b$ | NA | 1.0981 | 1.3769 | 0.8490 | NA | u-shaped |
| <i>Carapus bermudensis</i> | | | | | | | |
| | (1) $HL = y_0 + a \cdot IC$ | 0.4517 | 0.0506 | NA | 0.9675** | passed ($P = 0.9312$) | normal |
| | (2) $HL = a \cdot IC^b$ | NA | 0.2553 | 0.6488 | 0.9481** | passed ($P = 0.1201$) | funnel-shaped |
| | (3) $HL = \exp^a \cdot IC$ | NA | 0.0193 | NA | 0.8762 | passed ($P = 0.3737$) | funnel-shaped |
| | (4) $HL = y_0 + a \cdot IC + b \cdot IC^2$ | 0.5634 | 0.0228 | 0.0004 | 0.9719** | failed ($P = 0.0110$) | normal |
| | (5) $HL = a \cdot \ln IC - 0.3368$ | NA | 0.8921 | NA | 0.7773 | NA | u-shaped |

Models 1–5 are linear, power, exponential, quadratic, and logistic (*HL* head length; *IC* increment count; *NA* not applicable; the note of ** denotes significant $P < 0.0001$)

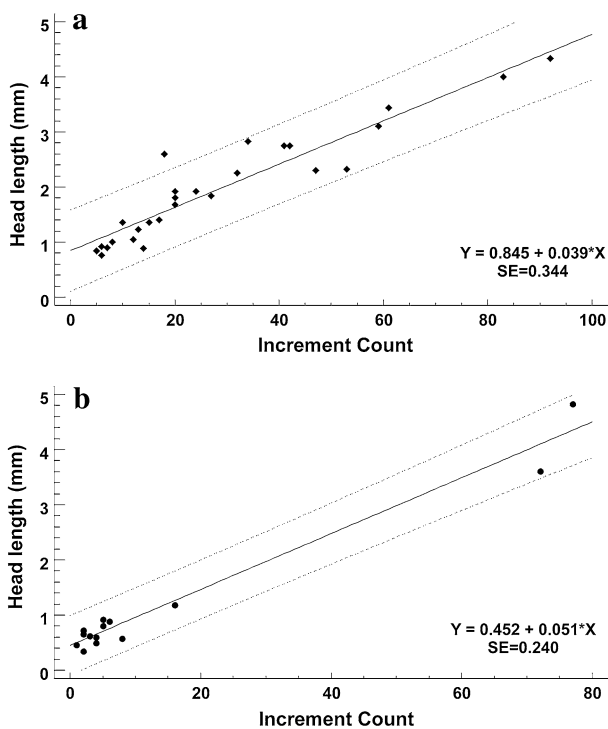


Fig. 6 Linear relations between head length and increment count in the vexillifer larvae of *Echiodon dawsoni* (a) and *Carapus bermudensis* (b) collected from the western North Atlantic (dashed lines indicate 95 % prediction limits; *SE* standard error)

similar to *Echiodon dentatus*, which absorbs yolk in 8 d and 7 mm TL (Brownell 1979). The first check in *C. bermudensis* was between increments 6 and 13 indicating completion of yolk absorption as early as 6 d, and 3.0 mm

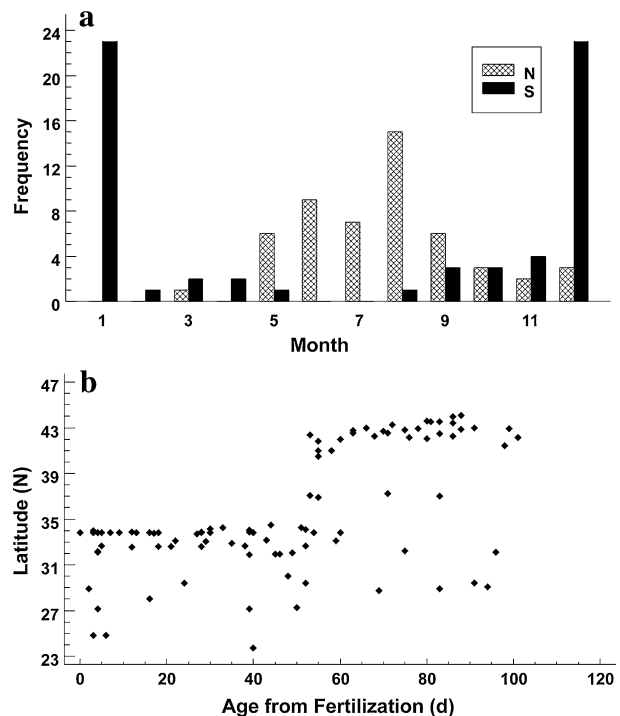


Fig. 7 Estimated spawning months of the vexillifer larvae of *Echiodon dawsoni* collected from the western North Atlantic. a Specimens collected north (N) and south (S) of 35°N latitude, b latitude of collection and estimated age from fertilization

TL. In *C. acus*, the yolk was completely absorbed in 3 d when vexillifers were 6 mm TL (Ehrenbaum 1905).

Second and third checks were not consistently observed. A transition zone that marks the end of the tenuis stage was

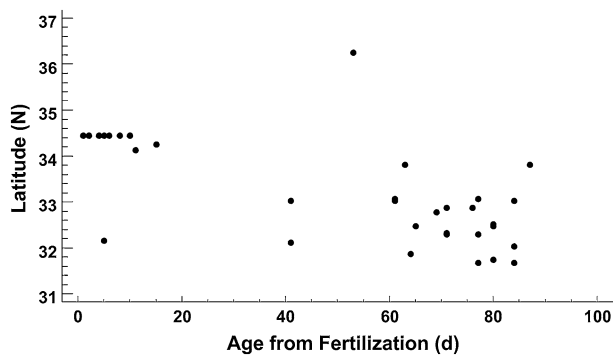


Fig. 8 Latitude of collection and estimated age from fertilization of the vexillifer larvae of *Carapus bermudensis* collected from the western North Atlantic

evident at the 49th and 83rd increments of *C. homei* and *C. boraborensis* (see Parmentier et al. 2002a, Parmentier et al. 2002b). The vexillifer of *Ec. dawsoni* with the oldest estimated AFF was 101 d and the oldest vexillifer of *C. bermudensis* had AFF of 77 d, which indicates vexillifer duration of up to about three months for both species.

Linear growth models were realistic, because HL and TL continued to increase and TL did not shrink in vexillifers (Parmentier et al. 2004a, b). From the linear model for *Ec. dawsoni*, estimated y_0 , the HL at hatching was 0.84 mm, which corresponds with 5.0 mm TL. One-day-old vexillifers of *Ec. dentatus* and *Ec. drummondii*, with a yolk sac, developing at temperatures 11–15 °C in the Mediterranean and eastern North Atlantic, were 5 mm in TL (Kennedy and Champ 1971; Brownell 1979). The TL of *Echiodon rendahli* from the South Pacific, incubated at 11.2 °C and hatched in 2.5 d, is 5 mm (Robertson 1975). From the linear model for *C. bermudensis*, y_0 was 0.45 mm HL, which corresponds to 3.0 mm TL. *Carapus acus* from the Mediterranean hatch in 3 d and are 6 mm in TL (Ehrenbaum 1905).

The Gulf Loop Current is the principal progenitor of the Gulf Stream, and these two currents (Fig. 1) are the vectors for the northward transport of fish larvae, including carapid vexillifers. The Gulf Loop Current has average velocities of 1.2 m s⁻¹ (Lugo-Fernández 2006) and the Gulf Stream has velocities of 1.5 m s⁻¹ (Olson et al. 1994). Velocities of the Gulf Loop Current and the Gulf Stream do not vary greatly seasonally (Lugo-Fernández 2006; Olson et al. 1994). The courses of the Gulf Loop Current and the Gulf Stream do vary, and this variation could influence the entrainment of vexillifers from off continental shelf spawning habitats into the body of these currents and hence their northward advection. The Gulf Loop Current makes northward excursions on a frequency that varies from 0 to 16 months, but with no evident seasonality (Lugo-Fernández and Badan 2007); consequently, variation in course does not predictably influence the entrainment of the

vexillifers of *Ec. dawsoni* into the body of the Gulf Loop current. The Gulf Stream flows approximately parallel to the 200 m isobath, but its course fluctuates east to west (Lee et al. 1989). The Gulf Stream path exhibits two states: weakly deflected when its course is more onshore, and strongly deflected when its course is more offshore (Lee et al. 1989). The weakly deflected state is more common in summer, while the strongly deflected state is more common in winter (Lee et al. 1989).

Echiodon dawsoni spawn every month of the year somewhere in the western North Atlantic (Fig. 7a). Lacking any estimate of age and growth, Markle and Olney (1990) suggested that spawning of *Ec. dawsoni* and *C. bermudensis* was seasonally protracted. If adrift for three months, water currents can transport vexillifers considerable distances from spawning sites in the Gulf of Mexico and off the southeastern U. S. The Gulf Loop Current can influence the outer shelf and slope of the northern Gulf of Mexico (Murphy and Hurlburt 1999), while the Gulf Stream influences the mid- and outer shelf off the southeastern coast of the U. S. (Olson et al. 1994) northward to the Nova Scotian shelf (Markle et al. 1980; Hare et al. 2002). Larval fishes spawned on the mid- and outer shelf can be entrained into the Gulf Loop Current in the Gulf of Mexico (Richards et al. 1989) or the Gulf Stream off the southeastern coast of the U. S. (Govoni 1993; Govoni and Spach 1999; Govoni et al. 2013). In 90 d, a larva travelling in the body of the Gulf Loop Current or the Gulf Stream at an average velocity of 1.2–1.5 m s⁻¹ could potentially cover 9,300 km, more than enough to go from the Gulf of Mexico to the Nova Scotian shelf.

There was also an indication of seasonal geographic pattern in spawning (Fig. 5a). Data indicate no spawning north of 35 °N, while all larvae north of 35 °N had been adrift for at least 55 d for *Ec. dawsoni* (Fig. 7b), enough time to travel 5,700 km, and so could have easily been spawned in the Gulf of Mexico. All of these collections contained single vexillifers, which indicates that vexillifers were well dispersed. South of 35 °N, especially off the southeastern U. S., the collecting effort was biased for winter months, while the frequency of capture of winter-spawned larvae was high, which likely reflected this bias. Off Nova Scotia, the collecting effort was more uniform, but most larvae caught were hatched from eggs fertilized from May to September (Fig. 5a). Encountering these larvae off Nova Scotia requires collecting in or near the Gulf Stream or Gulf Stream warm core eddies and would be largely haphazard given the inter-annual and seasonal variability of ocean currents. The origin(s) of *Ec. dawsoni* collected off Nova Scotia cannot be determined, because there are numerous ways for larvae to be entrained in the Gulf Stream: off the outer shelf in the northern Gulf of Mexico into the Gulf Loop Current by either warm core

(anticyclonic) or cold core (cyclonic) eddies (Lugo-Fernández 2006); off the outer shelf off the southeastern U. S. by small frontal eddies (Govoni 1993; Govoni and Spach 1999) or cold core eddies into the Gulf Stream (Govoni et al. 2013); or from off the northern Antilles, Bahamas, or Bermuda by warm core eddies (Murphy and Hurlburt 1999; Hare et al. 2002).

South of 35 °N, there were multiple age classes. Off the southeastern U. S., young larvae of both species were collected. Water on the mid- and outer continental shelf off the southeastern coast of the U. S. has a residual drift to the southwest with velocities in the order of 0.5 m s⁻¹ (Haight 1942; Govoni and Pietrafesa 1994) and indicates local spawning of both species. In contrast, Powell et al. (2000) collected no small vexillifers over reef habitats in Onslow Bay south of Cape Hatteras and suggested that the presence of large vexillifers of *Ec. dawsoni* and *C. bermudensis* was due to transport from reef habitats east of Florida and the Caribbean, where carapid vexillifers have been collected (Limouzy-Paris et al. 1994; Sponaugle et al. 2003, 2005). In the Onslow Bay area, both local retention and transport of older vexillifers from southern locations via the Gulf Loop Current and Gulf Stream north of Cape Hatteras are likely. A more offshore spawning location would subject vexillifers to highly energetic, rapidly moving, and generally northeastward currents (Hare et al. 2002; Lugo-Fernández 2006). In the Onslow Bay area, vexillifers of *Ec. dawsoni* were more commonly collected offshore, whereas the vexillifers of *C. bermudensis* were inshore over reef habitats. Consistent with increased advection due to spawning location, vexillifers of *Ec. dawsoni* were widespread and more common north of 35 °N than *C. bermudensis*.

Compared with *Ec. dawsoni*, most the vexillifers of *C. bermudensis* (all but one) were collected south of 35 °N, and many of these were young, the result of recent spawning (Fig. 8), in summer. Overall, these young vexillifers of *C. bermudensis* were collected at locations typically inshore of any of the influence of the Gulf Stream and its eddies, even in winter when the Gulf Stream is in its weakly deflected state. With more inshore spawning, the vexillifers of *C. bermudensis* are less affected by seasonal variation in the disposition of the Gulf Stream; the single vexillifer of *C. bermudensis* collected north of 35 °N was likely entrained into the Gulf Stream by propagating eddies (Govoni and Spach 1999; Govoni et al. 2013), swept northward, and stranded on the continental shelf by meanders and eddies downstream north of 35 °N (Hare et al. 2002).

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