



Research article

Diet of an underappreciated benthic intertidal fish, *Cryptacanthodes maculatus* (Cryptacanthodidae), in eastern Maine, USA

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Abstract: We discovered through gut-content analysis over a 20-month period (June 2009–March 2011) that a little-known benthic fish, the wrymouth, *Cryptacanthodes maculatus*, preyed upon soft-bottom fauna from 8 phyla, 10 classes, and 28 genera in the lower intertidal/ shallow subtidal zone in Cobscook Bay (eastern Maine, USA). Wrymouth (N = 42; total length = 30–50 cm) live infaunally in extensive subterranean burrows, and consumed mainly polychaetes and amphipods that occurred in 80% and 75% of stomachs, respectively. The two most common polychaetes, *Alitta virens* and *Harmothoe imbricata*, were found in 60% and 25% of stomachs, respectively. Gammarideans *Leptocheirus pinguis* and *Ampelisca abdita* were the two most common amphipods occurring in 40% and 33% of stomachs, respectively. Benthic core samples taken from the mid- and low shore were ambiguous in helping to understand where wrymouth forage. Wrymouth likely contribute to trophic linkages between the intertidal and subtidal zones in soft-bottoms; however, its relative role in regulating benthic community structure, aspects of its reproductive behavior, and early life-history is unknown due in part to its cryptic lifestyle. In addition to identifying components of the wrymouth's diet, we document gravid females for the first time, and when they appear in the population.

Keywords: *Cryptacanthodes maculatus*; wrymouth; fish; subtidal-intertidal; soft-bottoms; Maine; USA; benthic community

1. Introduction

Fish are important predators in rocky and soft-bottom intertidal environments, and have both direct and indirect effects on benthic community structure [1-5]. Experimental evidence [6-8] and indirect measures (i.e., diet studies [9-12]; stable isotopes [13,14]) typically are employed to estimate the role of these predators in regulating populations of benthic invertebrates. In New England, several species of small, predatory fish that forage intertidally during tidal inundation (e.g., *Fundulus heteroclitus heteroclitus* [L., 1766], *F. majalis* [Walbaum, 1792], *Gasterosteus aculeatus aculeatus* [L., 1758], *Menidia menidia* [L., 1766]) consume a variety of metazoan taxa such as small bivalves, crustaceans, gastropods, and polychaetes [15-16]. In addition, juveniles and adults of larger demersal fish (e.g., *Leucoraja ocellata* [Mitchill, 1815], *Microgadus tomcod* [Walbaum, 1792], *Pollachius virens* [L., 1758], *Pseudopleuronectes americanus* [Walbaum, 1792]), that are temporary or seasonal residents of the soft-bottom intertidal and shallow subtidal zone, consume a similar array of benthic infauna [17].

In eastern Maine, USA, the soft bottom benthos at/near the transition between the extreme lower intertidal and shallow subtidal is home to a little-known and studied eel-like predatory fish, the wrymouth, *Cryptacanthodes maculatus* [Storer, 1839] (Class Actinopterygii, Order Perciformes; Figure 1). This species is one of four in the family Cryptacanthodidae [18], and the only species in this family to reside in the Northwest Atlantic (the others are confined to the northern Pacific) with a distribution from New Jersey to southern Labrador, including Long Island Sound and the Gulf of St. Lawrence [19]. Like others in this family, *C. maculatus*, which can attain lengths of 90 cm [20], constructs an extensive system of irregular, branching subterranean tunnels (3–5 cm in diameter and up to 20 cm deep, B. Beal, pers. obs.). A single fish uses a main entrance (sometimes noticeably littered with shell fragments of blue mussels, *Mytilus edulis* [L., 1758], soft-shell clams, *Mya arenaria* [L., 1758], and/or common periwinkles, *Littorina littorea* [L., 1758]; [21], and several secondary (smaller) openings to access the tunnels (B. Beal, pers. obs.).



Figure 1. A female of *Cryptacanthodes maculatus* collected on 10 September 2010 from the extreme low water mark at the Boat Landing, Perry, Maine, USA. Total length = 38.0 cm. Scale = 1 cm.

Little is known about the natural history and ecology of *Cryptacanthodes maculatus*. To date, no records exist of its reproductive habits [22] or density, and few observations have been published regarding its diet. The earliest description of its gut contents was from Willey & Huntsman [23] who found gammaridean amphipods, *Gammarus* spp., sand shrimp, *Crangon septemspinosa* [Say, 1818], and fragments of winter flounder, *Pseudopleuronectes americanus*, in fish collected from tidal flats at the mouth of the Magaguadavic River, a tributary of Passamaquoddy Bay, New Brunswick, Canada. Scattergood [24] described two individuals of *C. maculatus* (75.7 and 69.6 cm total length, TL) caught in a commercial herring weir in Passamaquoddy Bay in 1947 that contained adults of herring (*Clupea harengus* [L., 1758]) and rainbow smelt (*Osmerus mordax* [Mitchell, 1814]), and juveniles of silver hake (*Merluccius bilinearis* [Mitchell, 1814]). A single individual (23 cm TL) taken from a bottom trawl survey in the Gulf of Maine contained only shrimp in the family Pandalidae [25]. The only other published account was from an intertidal mudflat in eastern Maine (Chandler River, Jonesboro) where the stomachs of ten fish (35–50 cm TL) revealed only individuals of *C. septemspinosa* [21].

Distribution and abundance patterns of *Cryptacanthodes maculatus* are poorly understood. Besides mudflats and shallow subtidal muddy bottoms in eastern Maine, individuals have been observed in tidal pools [26], and their larvae have been recorded in ichthyoplankton samples taken in Buzzards Bay, Massachusetts [27], and Narragansett Bay, Rhode Island [28]. Chenoweth [29] recorded wrymouth larvae in the upper Damariscotta River and Sheepscot River estuaries (central Maine) from January to June 1970. Juveniles and adults have been recorded only rarely in bottom trawl surveys (Casco Bay, Maine [30]; Brown's Bank, Gulf of Maine [31]; Scotian Shelf, Canada [32]). Tyler [33] used an otter trawl to survey fish populations monthly from March 1965 to June 1966 in a deep area (38–55 m) of Passamaquoddy Bay, and MacDonald et al. [34] used similar sampling methods in the same area, and at one offshore station in the Bay of Fundy over five years from 1976–1981. Both studies encountered wrymouth irregularly and in low numbers (one or two specimens over the entire sampling period). *C. maculatus* has been captured occasionally in deep water (>100 m) in the Gulf of Maine (160 m in Jeffrey's Bowl [35]; 250 m approximately 70 km northeast of Cape Cod, [36]), and a single individual was collected from a trap set for red crab, *Chaceon quinque-dens* [Smith, 1879], at a depth of 600 m in Block Canyon (ca. 150 km south of the Rhode Island coast [37]).

Although few published studies exist about consumers of *Cryptacanthodes*, birds, fish, and seals are among the suite of predators that feed on this benthic fish. Otoliths and/or other discernible pieces of the fish have been recovered from regurgitants of nestling double-crested cormorants, *Phalacrocorax auritus* [Lesson, 1831], on islands near Boothbay Harbor (central Maine [38]), in Penobscot Bay (eastern Maine [39]), and along the eastern shore of Nova Scotia [40]. Wrymouth larvae and juveniles were recorded in stomachs of Atlantic salmon smolts (*Salmo salar* [Linnaeus, 1758] sampled in Penobscot Bay from 2001 to 2005 [41]), and larger individuals have been recorded in the stomachs of Atlantic bluefin tuna (*Thunnus thynnus* [Linnaeus, 1758]) caught off New England during 1988–1992 [42]. Langton and Watling [43] found that wrymouth juveniles accounted for a high proportion of the diet of longhorn sculpin, *Myoxocephalus octodecemspinus* [Mitchell, 1814], in Sheepscot Bay (midcoast Maine). In addition, wrymouth comprised a “notable proportion” of thorny skate, *Amblyraja radiata* [Donovan, 1808], collected from bottom trawl surveys (1973–1998) covering continental shelf waters from Cape Hatteras, North Carolina to Nova Scotia [44]. Hammill [45] examined the diet composition of grey seals, *Halichoerus grypus*

[Fabricius, 1791], in the southern Gulf of St. Lawrence. *C. maculatus* individuals were found in ca. 8% of seal stomachs.

The objective of this study was to examine gut contents of wrymouth fish in far eastern Maine to determine the diversity of fauna consumed, and to elucidate whether these fish specialize on certain prey items or are generalist predators. We collected 42 individuals of *Cryptacanthodes maculatus* between July 2009 and March 2011 from the lower intertidal of a soft-bottom flat in eastern Maine, and compared fauna from fish stomachs to the fauna sampled from the same benthic intertidal community.

2. Materials and Methods

2.1. Sampling wrymouth fish

To assess gut contents and other attributes of *C. maculatus*, a total of 42 fish were sampled over approximately 20 months (Table 1). Fish were collected at low tide near the extreme low tide mark on spring tides at the northern end of East Bay near the Boat Landing in Perry (PBL), Maine, USA within Cobscook Bay (44.946286 N; -67.102342 W). This site is a wind-sheltered mudflat (ca. 0.53 km²) with a northeasterly orientation. The hydrodynamic forces are controlled by a semidiurnal lunar tide (M₂) with a 6.5 m range during spring tides. Sediment temperatures vary with seawater (-1 to 14 °C) and air (-30 to 30 °C) temperatures. The upper intertidal is comprised of cobble and large rock outcrops that are colonized by fucoid algae (*Ascophyllum nodosum* [L.] [Le Jolis, 1863]; *Fucus vesiculosus* [L., 1753]). On each sampling date, burrow entrances (distinct holes ranging in size from 3–9 cm) were located on the mudflat surface. (No burrow entrances were observed above the lowest intertidal level.) To sample fish, burrows and their associated tunnels were collapsed by walking on and around them. Fish were captured by hand after they surfaced (ca. 5–10 minutes), placed into separate plastic bags, added to ice-filled, insulated coolers, and then taken to the University of Maine at Machias (UMM) (within 90 minutes) where most were processed immediately to reduce the likelihood of gut content spoilage or complete digestion. (Alternative methods to capture fish during low tide -- digging adjacent to burrows using clam hoes, placing hands inside burrows -- proved unsuccessful.) Individuals that could not be processed immediately were stored in a cold room (4 °C) and processed within 8 hours. Total length (TL, to the nearest 0.5 cm) and sex were recorded for each individual. The gastrointestinal tract from pharynx to anus of each fish was dissected and stored in 5% buffered formalin. Organisms in the gut were identified to genus and species if possible; otherwise, the presence of pieces (e.g., scales, otoliths, acicula, epidermis, jaws, etc.) aided in discerning Phyla and sometimes Class.

For each of the 25 individuals collected in 2010 and 2011, gonad mass was recorded to the nearest 0.1 g. In addition, the two largest otoliths (sagittae) were removed from each fish. Because information from both sagittae from an individual fish may not yield independent data, one otolith from each fish was chosen randomly and measured to the nearest 0.1 mm using Vernier calipers, dried at room temperature, immersed in mineral oil, and bands counted from the edge of the nucleus to the edge of the nearest annulus under a dissecting microscope at 10× magnification. A random subset of examined otoliths was validated by a fish aging specialist (P. J. McDonald, Associate, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, Washington 98112;

Patrick.J.McDonald@noaa.gov). Although distinct bands were observed in the otoliths, and these appeared similar to the annuli of other fish species (P. McDonald, pers. comm.), it is unknown whether the bands represent annual markings, seasonal or migration events because no studies have been published to date on wrymouth aging. Therefore, reference to the number of bands per otolith is used here rather than annuli or years.

Table 1. Date and number of wrymouth fish sampled from the Perry Boat landing, sex ratio, and when gonad mass was recorded. Benthic cores refer to samples (Area = 0.01824 m²; depth = 15 cm) taken at the mid (n = 27) and lower (n = 27) intertidal zone. - = no data; √ = samples taken.

Date	No. Fish captured	♂:♀	Otoliths sampled	Gonad mass	Benthic cores
26 May 2009	-	-	-	-	√
26 June 2009	11	9:2	-	-	-
21 August 2009	6	5:1	-	-	-
8 October 2009	-	-	-	-	√
10 September 2010	10	8:2	√	√	-
8 October 2010	1	1:0	√	√	-
7 November 2010	10	6:4	√	√	-
20 March 2011	4	1:3	√	√	-

2.2. Benthic Sampling for Resident Infauna

Concurrent with wrymouth sampling, we were investigating distribution and abundance of benthic macroinvertebrates at nine intertidal locations within Cobscook Bay (B. Beal, unpubl. data). Because one of those sites included PBL, we present data from two sampling dates (Table 1) to determine whether macroinvertebrates found in the guts of *C. maculatus* could possibly have come from the soft-bottom intertidal at PBL. On each date, 27 cores were taken at low tide near the mid (+0.5 m; 44.947999 N; -67.102917 W) and lower (-0.2 m; 44.946286 N; -67.102342 W) tidal level. A 300 m transect was placed parallel to the low water mark at both tidal heights, and divided into three approximately equal blocks 100 m × 1 m. Within each block, a 1-m² quadrat was tossed haphazardly at approximately 30 m intervals, and within each quadrat, three benthic cores were taken from the center of three of the four equal-sized quadrants. Samples (a = 2 dates, b = 2 tidal heights, c = 3 blocks per tidal height, d = 3 quadrats per block, and n = 3 cores per quadrat; N = 108) were processed at UMM within three hours by gently washing each through a 1 mm sieve with freshwater. Contents of each sample was preserved using 5% buffered formalin and stained with Rose Bengal to aid in locating fauna within the residue using white enamel pans in the laboratory. Fauna from each sample was identified to species when possible and enumerated. The World Register of Marine Species (www.marinespecies.org) was consulted for species names and their authority. Sediment samples, taken on 26 May 2009 at both tidal heights (n = 2) using a coring device (A = 0.005 m² to 15 cm) and processed according to Folk [46], showed a well-sorted muddy sand substrate with a combined mean grain size ($\pm 95\%$ CI) of $3.45 \pm 0.76 \phi$.

2.3. Statistical analyses

2.3.1. Wrymouth morphometrics and gut contents

Differences in size-frequency distribution of *C. maculatus* across dates and by gender were assessed using a Fisher's exact test. Fish total lengths were divided into four 5 mm increments across the size range (30–50 cm). A two-way, fully factorial ANOVA was used to test for the interactive effects of sampling date and gender on mean TL. Sex ratio, under the null hypothesis of 1♀:1♂, was tested using a chi square goodness-of-fit test. A lack-of-fit test was conducted on the relationship between gonad mass and sampling date for both genders. Effects of gender and sampling date on wrymouth gut contents were analyzed using nonparametric multivariate techniques (NMDS 2D ordination plots) on Bray-Curtis similarity measures for presence/absence data. Multivariate statistical analyses were run in PRIMER 6.0 and permutational multivariate analysis of variance (PERMANOVA, 9999 permutations, type III SS, and unrestricted permutation of raw data) using a completely factorial linear model with two fixed factors (sampling date and gender). All possible pairwise comparisons ($k = 15$) were conducted on the sampling date factor using a Bonferoni correction which yielded an adjusted type I error rate ($\alpha' = 0.0034$). SIMPER analysis also was used to determine dissimilarities in gut contents between sampling dates.

2.3.2. Resident macroinvertebrate infauna

Mean number of species (S), diversity (Shannon-Weiner, $H' [\log_e]$), and Pielou's evenness (J') from benthic cores were analyzed using univariate statistical methods. The following linear model was used to carry out the ANOVA's:

$$Y_{ijkl} = \mu + A_i + B_j + AB_{ij} + C(AB)_{k(ij)} + D(ABC)_{l(ijk)} + e_{m(ijkl)}$$

where:

Y_{ijkl} = dependent variable (S , H' , J'),

μ = theoretical mean,

A_i = Date (26 May vs. 8 October 2009; factor is fixed),

B_j = Tide height (Mid vs. Low; factor is fixed),

C_k = Block (1, 2, 3; factor is random),

D_l = Quadrat (1, 2, 3; factor is random), and,

e_m = Experimental error.

All F-tests followed the Cornfield-Tukey rules [47]. Analyses were performed using SAS for Windows (v. 9.2) on the untransformed data after testing for normality (Shapiro-Wilk test) and variance homogeneity (Levene's test). A Type I error rate (α) of 0.05 was used for all analyses. Means are accompanied by 95% confidence intervals unless otherwise stated.

Community abundance data were analyzed using nonparametric multivariate techniques [48]. NMDS based on Bray-Curtis similarities were plotted into 2D ordination plots using both the

untransformed (where dominant species have a high influence) and fourth root-transformed (where high abundance species are downweighted) abundance data [49]. An analysis of multivariate dispersion (MVDISP) was performed to determine which tidal height was most variable with respect to species abundance. Multivariate statistical analyses were run in PRIMER 6.0 and PERMANOVA (as described above) using the linear model described above. Regardless of the outcome of PERMANOVA, SIMPER (similarity percentage) analysis was used to explore aspects of abundance of species within and between tidal heights. A posteriori pairwise comparisons used a conservative Type I error rate ($\alpha' = [1 - \alpha]^{1/n}$, where $\alpha = 0.05$ and $n =$ number of comparisons; [50]).

2.3.3. Relationship between wrymouth gut contents and benthic macroinvertebrates

To determine if gut contents from fish were representative of the benthos at the mid and low intertidal at PBL, NMDS based on Bray-Curtis similarities were plotted into a 2D ordination plot using presence/absence data for core samples and fish gut contents.

3. Results

3.1. Wrymouth gut contents

Guts in 40 of 42 (ca. 95%) fish contained at least one identifiable item. Fauna from eight phyla, ten classes, and 28 genera were identified (Table 2). Annelids (all polychaetes) occurred in 35 of 42 (83.3%) guts, and arthropods (mainly amphipods) were found in 31 of 42 stomachs (73.8%; Table 2). Ten polychaete genera were identified among the fish collected. The two most common polychaetes (both carnivorous), *Alitta virens* [M. Sars, 1835] and *Harmothoe imbricata* [L., 1767], were found in 59.5% (25/42) and 26.1% (11/42) of fish stomachs, respectively. Nine species of amphipods, two species of mysid shrimp, one isopod, and one decapod were among the arthropods identified in fish stomachs. *Leptocheirus pinguis* [Stimpson, 1853] (16/42 = 38.1%) and *Ampelisca abdita* Mills, 1964 (14/42 = 33.3%), both gammaridean amphipods, were the two most common arthropods, respectively (Table 2). Nematodes, nemerteans, and platyhelminthes were found in stomachs from the two sampling dates in 2009, but none were found in samples from 2010–2011. Two species of demersal fish (both intact), the short-horned sculpin, *Myoxocephalus scorpius* [L., 1758], and the three-spined stickleback, *Gasterosteus aculeatus aculeatus*, were found in one and three wrymouth individuals, respectively (Table 2). In addition, otoliths and scales occurred in 12 fish (28.6%). NMDS plots showed no obvious separation between wrymouth genders and only weak groupings for collection date (Figure 2). PERMANOVA revealed no significant difference for gender ($P = 0.3018$) but did for sampling date (0.0034); however, no pairwise comparison was statistically significant. The comparison between August 2009 and November 2010 was the only one that was nearly significant ($P = 0.0051$, using $\alpha' = 0.0034$). SIMPER analysis on the same data indicated that the average dissimilarity between these two sampling dates was 81.6%.

Table 2. Gut contents of *Cryptacanthodes maculatus* from 42 fish collected from June 2009 to March 2011 at the Boat Landing, Perry, Maine, USA. (x = presence; - = not observed). Number in parentheses is the number of fish containing that particular prey item in the gut in that collection. Size range and gender ratio by collection date: 2009 (26 June [30.0 to 50.0 cm; 9♂:2♀], 21 August [36.5 to 44.0 cm; 5♂:1♀]); 2010 (10 September [36.0 to 45.0 cm; 8♂:2♀], 8 October [40.5 cm; 1♂], 7 November [38.0 to 46.0 cm; 6♂:4♀]); 2011 (20 March [39.5 to 42.0 cm; 1♂:3♀]).

	26 June (n = 11)	21 August (n=6)	10 September (n=10)	8 October (n=1)	7 November (n=10)	20 March (n=4)
Annelida						
<u>Polychaeta</u>						
<i>Alitta virens</i> [M. Sars, 1835]	x(7)	x(4)	x(2)	x(1)	x(7)	x(4)
<i>Eteone</i> spp.	-	x(1)	-	-	-	-
<i>Fabricia stellaris</i> [Müller, 1774]	x(1)	x(1)	-	-	-	-
<i>Hartmania moorei</i> [Pettibone, 1955]	-	-	x(3)	x(1)	x(5)	x(1)
<i>Harmothoe imbricata</i> [L., 1767]	x(1)	-	-	-	-	-
<i>Lumbrineris</i> spp.	x(1)	-	-	-	-	-
<i>Neoamphitrite johnstoni</i> [Dalyell, 1853]	x(1)	x(1)	-	-	-	-
<i>Ophelina acuminata</i> [Örsted, 1843]	x(2)	-	-	-	x(4)	x(1)
<i>Polydora</i> spp.	x(1)	x(1)	-	-	-	-
<i>Pygospio elegans</i> [Claparède, 1863]	-	x(1)	-	-	-	-
Pieces ¹	x(3)	x(4)	-	-	-	-
Arthropoda						
<u>Malacostraca</u>						
<i>Ampelisca abdita</i> [Mills, 1964]	x(1)	-	x(2)	x(1)	x(8)	x(2)
<i>Corophium volutator</i> [Pallas, 1766]	x(1)	-	-	-	-	-
<i>Crangon septemspinosa</i> [Say, 1818]	-	x(1)	x(1)	-	-	-
<i>Edotia triloba</i> [Say, 1818]	-	-	-	x(1)	x(1)	-
<i>Gammarus oceanicus</i> [Segestråle, 1947]	-	-	-	-	-	x(2)
<i>Gammarus mucronatus</i> [Say, 1818]	-	-	-	-	x(1)	-
<i>Leptocheirus pinguis</i> [Stimpson, 1853]	x(5)	x(1)	x(4)	-	x(4)	x(2)
<i>Neomysis americana</i> [S.I. Smith]	-	-	-	-	x(2)	-
<i>Orchestia gammarellus</i> [Pallus, 1766]	-	-	-	-	x(1)	-
<i>Phoxocephalus holbolli</i> [Krøyer, 1842]	x(2)	-	-	x(1)	x(5)	x(2)
<i>Pontoporeia femorata</i> [Krøyer, 1842]	x(3)	-	x(1)	x(1)	x(4)	-
<i>Praunus flexuosus</i> [Müller, 1776]	-	-	x(2)	-	x(2)	-
<i>Unicola irrorata</i> [Say, 1818]	-	-	-	-	x(1)	-
Unidentified	x(3)	x(2)	-	-	-	-

Maxillopoda

Unidentified copepods	-	x(1)	-	-	-	-
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Ostracoda

Unidentified ostracod	-	-	-	-	-	x(2)
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Chordata**Actinopterygii**

<i>Gasterosteus aculeatus aculeatus</i>	-	-	x(1)	-	x(2)	-
<i>Myoxocephalus scorpius</i> [L., 1758]	-	x(1)	-	-	-	-
Unidentified scales, otoliths	x(5)	-	x(1)	-	x(5)	x(1)

Echinodermata**Holothuroidea**

<i>Molpadia borealis</i> [Sars M, 1859]	x(1)	-	-	-	-	-
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Mollusca**Bivalvia**

<i>Mya arenaria</i> [L., 1758]	-	x(1)	-	-	-	x(1)
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Nematoda**Adenophorea**

Unidentified	x(9)	x(2)	-	-	-	-
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Nemertea**Anopla**

<i>Lineus ruber</i> [Müller, 1774]	-	x(1)	-	-	-	-
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Platyhelminthes**Trematoda**

Unidentified	x(6)	-	-	-	-	-
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¹ e.g., acicula, epidermis, jaws

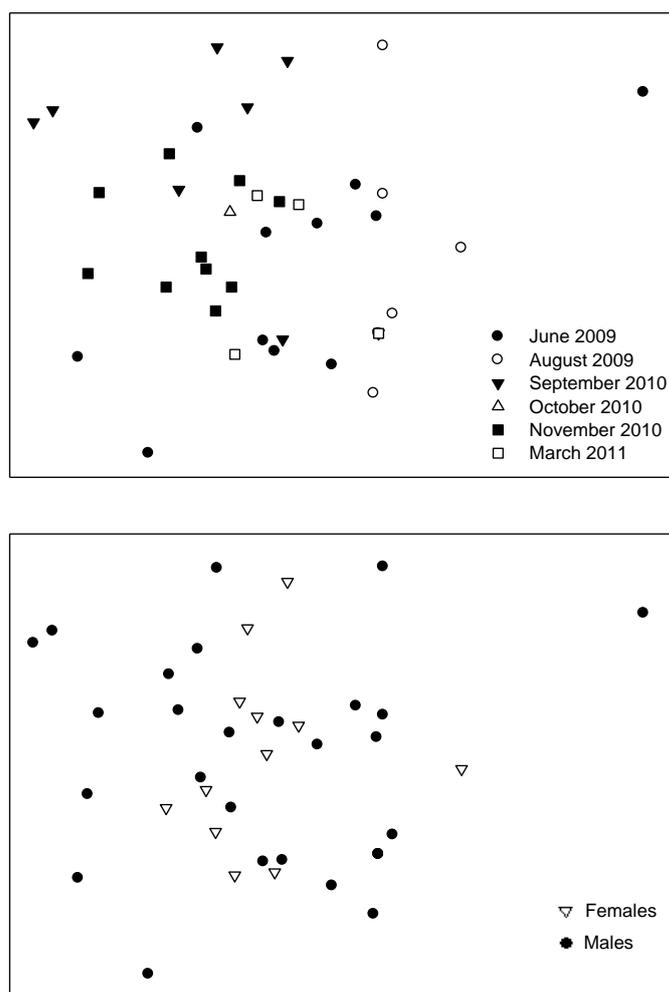


Figure 2. Multidimensional scaling (MDS) of 40 wrymouth fish according to the composition of their gut contents expressed by Bray-Curtis similarity index using species presence/absence data (Table 2). Fish were collected at the Boat Landing, Perry, Maine, USA from June 2009 to March 2010. Two fish were removed from the data because their guts were empty. Stress = 0.15.

3.2. Resident infauna

A total of 63 species were identified among the 108 benthic samples taken at PBL (52 and 45 from May and October 2009, respectively, with 35 species in common between the two sampling dates—35/63, 55.6%; Table S1). In May, 7 and 13 species were found exclusively in the mid- and lower intertidal, while in October, 8 species were found exclusively from both tidal heights. The majority of species from all samples were Annelids (34 or 53.9%) and Arthropods (17 or 26.9%), with 32 species of polychaetes and 12 species of amphipods (Table S1). Of the 35 common species between the two sampling dates, 21 (60.0%) were Annelids and 8 (22.9%) Arthropods.

Mean diversity (1.78 ± 0.05) did not differ significantly between sampling dates ($P = 0.65$) or tidal heights ($P = 0.36$), nor did mean number of species per core (11.57 ± 0.52 ; $P_{\text{Date}} = 0.19$;

$P_{\text{Tide height}} = 0.07$). Mean evenness varied significantly across tidal heights ($P = 0.04$; $\bar{x}_{\text{Mid}} = 0.77 \pm 0.02$ vs. $\bar{x}_{\text{Low}} = 0.70 \pm 0.03$, $n = 54$) but not across dates ($P = 0.80$). NMDS plots (Figure 3) showed different patterns based on whether abundance data were transformed. The untransformed abundance data (Figure 3a) had a lower stress value and showed more overlap between tidal heights and sampling dates than did the transformed data (Figure 3b), but in both instances, samples taken from the low tide area were more widely dispersed than samples from the mid tide (MVDISP with relative indices of multivariate dispersion for untransformed abundance data was 0.941 [mid] and 1.059 [low] vs. 0.98 [mid] and 1.02 [low] for transformed data). PERMANOVA revealed a significant difference between sampling dates and tidal heights, but not the interaction of these two factors on both untransformed ($P_{\text{Date}} = 0.003$; $P_{\text{Tide height}} = 0.01$) and transformed ($P_{\text{Date}} = 0.011$; $P_{\text{Tide height}} < 0.001$) species abundance data. SIMPER identified seven species that generated the most dissimilarity (55.5%) between tidal heights and six species that generated the most dissimilarity between sampling dates (58.9%; Table 3).

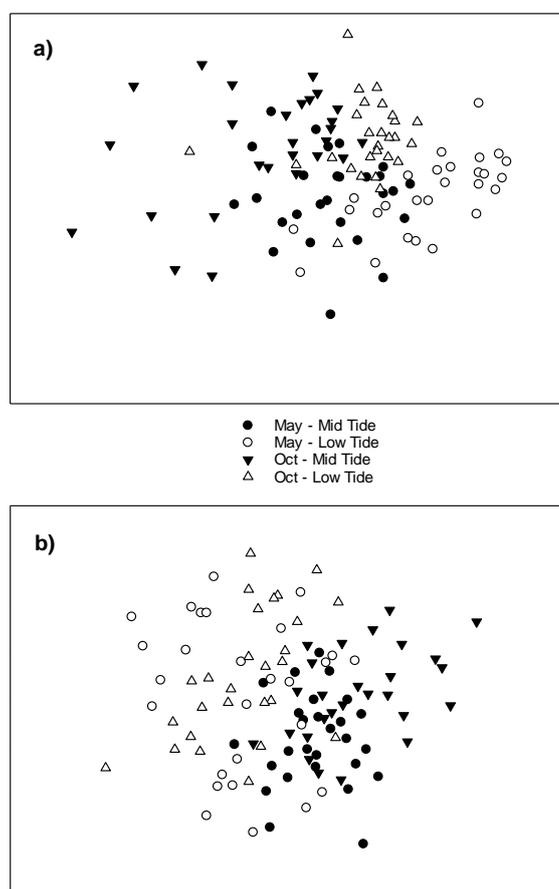


Figure 3. Multidimensional scaling (MDS) of benthic core data (Bray-Curtis similarity index) collected near the mid ($n = 27$) and low ($n = 27$) intertidal at the Boat Landing, Perry, Maine on 26 May and 8 October 2009. a) Untransformed abundance data (Stress = 0.21); b) Fourth root-transformed data (Stress = 0.26).

Table 3. Results of SIMPER analysis for infauna sampled from the mid and low intertidal height at the Boat Landing, Perry, Maine, USA on 26 May 2009 and 8 October 2009. Mean abundance, mean dissimilarity (\pm SD), and percent contribution to dissimilarity of individuals per core ($A = 0.0182 \text{ m}^2$, $n = 54$); Mean percent contribution of all taxa to average dissimilarity between the two tidal heights (a) was 58.1%, and 58.9% between sampling dates (b). Only taxa that contributed up to a total of 75% to the separation of the groups are listed.

a)				
Taxa	Mean abundance		Mean Dissimilarity	Contribution
	Mid	Low		
<i>Pontoporeia femorata</i>	15.15	27.19	11.09 (1.16)	19.10
<i>Phoxocephalus holbolli</i>	16.70	17.59	9.84 (1.29)	16.94
<i>Ecobia truncata</i> [Vanatta, 1924]	16.61	2.26	9.06 (1.07)	15.60
<i>Ampelisca abdita</i>	13.43	4.72	6.34 (1.08)	10.91
<i>Tubificoides</i> spp.	7.26	4.81	4.75 (0.68)	8.18
<i>Corophium volutator</i>	3.54	0.04	2.33 (0.48)	4.02
<i>Polydora cornuta</i> [Bosc, 1892]	2.65	1.54	1.68 (0.78)	2.90
b)				
Taxa	Mean abundance		Mean Dissimilarity	Contribution
	May	Oct		
<i>Phoxocephalus holbolli</i>	7.48	26.81	12.57 (1.53)	21.33
<i>Pontoporeia femorata</i>	25.20	17.13	10.30 (1.18)	17.48
<i>Ecobia truncata</i>	9.87	9.00	7.75 (10.97)	13.51
<i>Ampelisca abdita</i>	4.28	13.87	6.66 (1.07)	11.30
<i>Tubificoides</i> spp.	1.93	10.15	5.15 (0.69)	8.73
<i>Corophium volutator</i>	0.61	2.96	2.19 (0.43)	3.72

3.3. Relationship between wrymouth gut contents and resident fauna

Gut contents of fish were compared to the extant, adjacent intertidal benthic community (Figure 4). The percent overlap was ca. 25% (15 species in fish stomachs were in common with the 63 species from benthic cores). Of the fourteen identifiable species in fish stomachs that also occurred in the May 2009 benthic cores (6 polychaetes, 5 amphipods, an isopod, bivalve, and nemertean), eight occurred at both tidal heights (2 polychaetes, 5 amphipods, and a bivalve), four occurred only in low intertidal cores (3 polychaetes and a nemertean), and two in only mid intertidal cores (a polychaete and an isopod). Twelve species from the October 2009 cores occurred in fish stomachs (4 polychaetes, 7 amphipods, and a bivalve). Two polychaetes occurred at both tidal heights, and the other two occurred at only one tidal height. Five of the amphipods occurred at both tidal heights, while the other two occurred at the mid intertidal. The bivalve, *M. arenaria*, occurred at both tidal heights. Besides the two species of demersal fish (*M. scorpius* and *G. aculeatus aculeatus*) that typically would not have occurred in the benthic cores, eight other identifiable species (1 polychaete, 4 amphipods, 2 mysid shrimp, and a nemertean) were found in wrymouth stomachs, but not in benthic cores (Tables 2, S1).

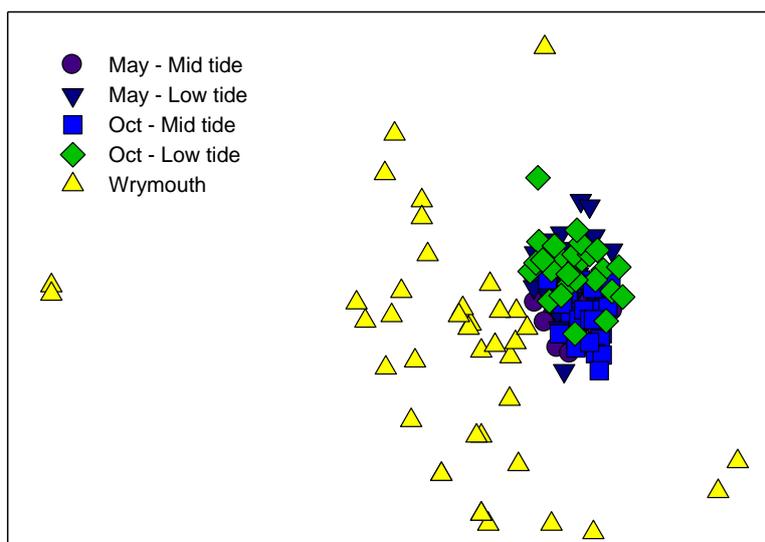


Figure 4. Non-metric multidimensional scaling (MDS) plot (stress = 0.16) based on Bray-Curtis similarity index using species presence/absence data for stomach contents of 40 wrymouth fish collected from 2009 to 2011 at PBL compared to the benthic organisms from 27 core samples taken near mid and low tide at that site during May and October 2009 (N = 108). PERMANOVA indicated a significant difference ($P = 0.001$) between fish diet and the resident benthos.

3.4. Wrymouth size-frequency, sex ratio, gonad mass, and otoliths

Size frequency distribution of fish varied significantly across sampling dates (Table 4), but not between genders ($P = 0.2330$). Mean TL (39.7 ± 1.3 cm, $n = 42$) did not vary significantly by date ($P = 0.9442$) or gender ($P = 0.4534$). The overall sex ratio ($30\text{♂}:12\text{♀}$) was significantly different from 1:1 ($\chi^2 = 7.714$, $df = 1$, $P = 0.005$). Both females collected in September 2011 were gravid (gonad mass of Female 1 [38.0 cm TL] and 2 [41.0 cm TL] = 17.5 g and 26.9 g, respectively; Figure 5). No other females sampled before or after September 2010 were found with eggs. Counts of distinct bands from each of the 25 otoliths were regressed on TL, and no significant correlation was observed ($r^2 = 0.0064$, $P = 0.704$, $n = 25$). Distribution of the number of bands per otolith ranged from 4 to 9 (median = 7.0, $\bar{x} = 6.3 \pm 0.5$ bands). A two-sample t-test (Levene's test: $P = 0.052$; Shapiro-Wilk test: $P > 0.05$) on mean number of bands per otolith indicated no significant difference between gender ($t = 1.84$, $df = 23$, $P = 0.079$).

Table 4. Size-frequency distribution of wrymouth fish (total length) collected over six dates from June 2009 to March 2011 at the Boat Landing, Perry, Maine, USA.

Date	Size-Class (cm)				Total
	30.0–34.9	35.0–39.9	40.0–44.9	45.0–50.0	
26 June 2009	4	4	-	3	11
21 August 2009	-	3	3	-	6
10 September 2010	-	3	5	2	10
8 October 2010	-	-	1	-	1
7 November 2010	-	2	7	1	10
20 March 2011	-	1	3	-	4
Total	4	13	19	6	42

Fisher's Exact Test—Size distribution varied significantly across sampling dates ($P = 0.0275$; $df = 15$).

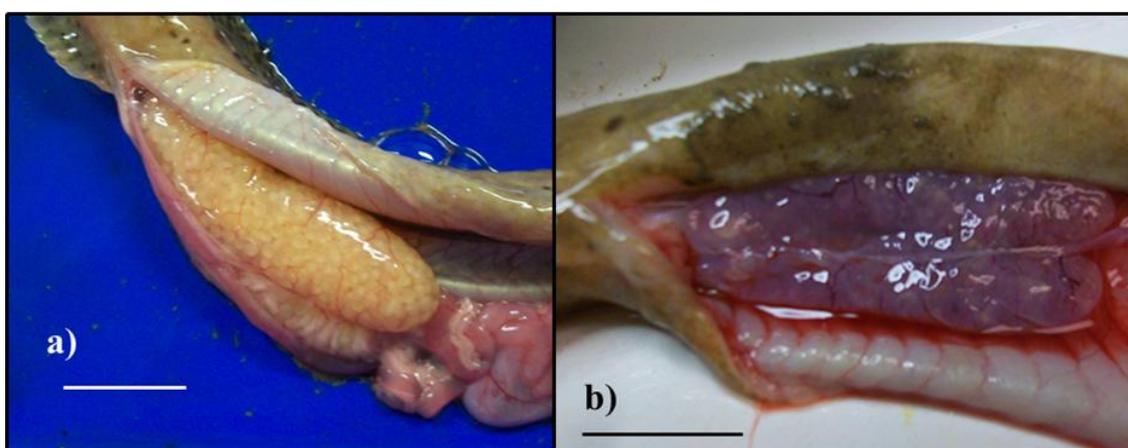


Figure 5. Females of *C. maculatus* collected from the Perry Boat Landing. a) Gonad with unfertilized eggs (10 September 2010; 41 cm TL; gonad mass = 26.9 g); b) Gonad without eggs (7 November 2010; 41.5 cm TL; gonad mass = 0.8 g). Ovary mass decreased according to a quadratic model from September 2010 to March 2011 ($Y = 26.2 + 0.2x - 4.2x^2$, $r^2 = 0.936$, $n = 9$, $P = 0.0003$) when mean mass was 1.47 ± 0.86 g ($n = 3$), whereas no significant change in the mass of testes occurred over that same period ($r^2 = 0.365$, $n = 16$, $P = 0.0523$; $\bar{x} = 0.39 \pm 0.19$ g). Scale in both sections = 1 cm.

4. Discussion

Our data shows conclusively that the population of wrymouth fish, *Cryptacanthodes maculatus*, an infaunal resident of soft bottoms near the extreme low intertidal and extending into the shallow subtidal zone at the Perry Boat Landing within Cobscook Bay in eastern Maine, USA, preys on soft-bottom residents. While it is unclear whether this benthic predator feeds preferentially in the intertidal or subtidal zone (Figure 4), it appears that fish at PBL are generalist feeders (Table 2), and that they may play an important, yet heretofore unrecognized, role in organizing the benthic intertidal and/or subtidal community.

4.1. Gut contents

A total of 25 taxa from the stomachs of fish were identified to species (Table 2), including mobile epibenthic species such as fish (*Gasterosteus* and *Myoxocephalus*) and a decapod caridean shrimp (*Crangon*) as well as mobile and sedentary infaunal (mainly polychaetes and amphipods). In addition, several bivalves, gastropods, echinoderms, copepods, ostracods, nematodes (Adenophorea), and trematodes were found in wrymouth stomachs, as well as a single nemertean species. Benthic cores taken from two intertidal heights at PBL in May and October 2009 (Table 1) identified 63 species of benthic macrofauna (Table S1). If the same suite of species were present at PBL across all fish sampling dates, then wrymouth gut contents indicate that these fish could be preying on organisms from at least the lower- and mid-tide levels during tidal inundation, and that foraging may extend to higher shore levels. For example, the amphipod *Gammarus oceanicus* was found in two of four fish stomachs in March 2011 (Table 2). While this species can be found among soft bottoms in eastern Maine [51], in Cobscook Bay it is found typically along the upper intertidal shore associated with or under rocks covered with macroalgae *Fucus* spp. and *Ascophyllum nodosum* (B. Beal, pers. obs. [52]), and along rocky shores in other areas of the northwest Atlantic [53]. In addition, the sabellid polychaete, *Fabricia stellaris*, was identified in two fish stomachs (Table 2), but was absent from the intertidal benthic cores (Table S1). In Europe, this species usually occurs near the upper intertidal [54], and in Maine can be found in rockweed-dominated low energy rocky shores [52]. Similarly, the beach-hopper, *Orchestia gammarellus*, found in one wrymouth stomach (November 2010, Table 2) but not in benthic cores, typically inhabits the littoral fringe along shores of the north Atlantic [55]. The upper shore of PBL is rocky, and covered with several species of fucoid macroalgae; hence, it is possible that foraging occurs at that shore level during tidal inundation of the mudflat. Conversely, wrymouths may forage subtidally. Wildish & Peer [56] sampled the sublittoral benthos at 98 stations in the lower Bay of Fundy and recorded six species that occurred in wrymouth stomachs in this study (*Harmothoe imbricata*, *Ophelina acuminata*, *Unciola irrorata*, *Leptocheirus pinguis*, *Phoxocephalus holbolli*, *Molpadia borealis*).

Gut contents provide only indirect evidence of predatory activities because it may be likely that wrymouth are secondary or even tertiary consumers. For example, several predatory polychaetes (e.g., *A. virens*, *H. imbricata*, *Lumbrineris* spp.) found in wrymouth stomachs consume small crustaceans and other small polychaetes [57,58]. In addition, the three-spined stickleback, *G. aculeatus aculeatus*, and the shorthorn sculpin, *M. scorpius*, are consumers of benthic polychaetes, crustaceans, copepods, and gastropods [59,60]. Therefore, the wrymouth diet may not be as broad as suggested from Table 2. We are aware of only four published reports on predatory activities of *C. maculatus*, and each used indirect evidence (gut contents) to determine feeding behavior. Only two of these studies [21,23] examined fish (35–40 cm TL) captured in the intertidal zone (eastern Maine and western New Brunswick, Canada, respectively), but neither discovered the diversity of organisms encountered in fish collected at our study site. One other investigation sampled fish regularly from March to September 2002 at two low intertidal sites near Jonesport (eastern Maine) (M.G. Kraus, Univ. Me. Machias, pers. comm.). Stomachs were relatively empty until May, with the most prominent prey items (*Crangon septemspinosa* and *A. virens*) in stomachs from June to September.

4.2. Natural history

The range of *C. maculatus* sizes collected at our study site over the 20-month period was narrow (30.0 to 50.0 cm, Table 2). If regularly occurring bands in the otoliths prove to be annuli then the putative age range of fish also was narrow (4–9 years). No juveniles were collected or observed at our study site within or near the burrows of larger fish, and it is unclear whether the lower intertidal/shallow subtidal soft-bottom habitat is suitable for young-of-the-year or juveniles. We have attempted to dig down into wrymouth burrows at PBL and other mudflats in eastern Maine using handheld clam hoes (as described in [61]) and other similar devices to capture fish of any size, but with no success. We conclude, hesitantly, that the lower intertidal/shallow subtidal where we have sampled burrows is not a nursery site for juvenile fish. This may be due to the lack of suitable prey as many predatory fish undergo ontogenetic shifts in diet with increasing size/age [62]. Or, the habitat at our study site may be too dangerous for young wrymouth. We have observed gulls (*Larus* spp.) at our study site, and at other mudflats in eastern Maine, consuming whole wrymouths over the range of sizes collected here when fish, for no apparent reason, suddenly appear wriggling at the sediment surface.

We document the first observation of *C. maculatus* eggs (unfertilized, and from both females collected in September 2010, Figure 5). No eggs were observed before or after this time, so we conclude that wrymouth at our study site released their eggs sometime between our early September and early November sampling dates. We do not know whether eggs are fertilized internally, as occurs in some species of the suborder Zoarcoidei [63], or released and subsequent fertilization occurs externally in burrows or elsewhere. In addition, it is unclear if parental care or guardianship of eggs and/or embryos, a common behavior in benthic zoarcoid fishes, occurs [64]; however, several lines of evidence suggest that larvae spend little or no time in the benthos, and that our observations concerning a late summer-early fall spawning are consistent with observations of planktonic larvae from other studies. For example, Chenoweth [44] collected *C. maculatus* larvae from eight stations in the upper Damariscotta and Sheepscot Estuary (midcoast Maine) as early as January 1970, with greatest numbers in trawls (ca. 100/30 min tow; 0.5 m net with 2 mm mesh) occurring in March 1970. Larvae in that study were collected as late as June 1970. More recently, Lazzari [65] sampled larval fish abundance in Penobscot Bay (eastern Maine). From April to June 1997, wrymouth larvae occurred in 12% of 102 samples (0.054/100 m³; 1.0 m net with 333-micron mesh), and in 33% of 40 samples collected from March to April 1998 (0.294/100 m³). Herman [28] collected a single larval wrymouth (20 mm TL) in Narragansett Bay (Rhode Island) in March 1958. Little information exists about reproductive behavior and subsequent distribution of larvae in the three congeners (*C. aleutensis* [Glibert, 1896], *C. bergi* [Lindberg, 1930], *C. giganteus* [Kittlitz, 1858]). Antonenko et al. [18] indicated that ovaries from females of *C. bergi* collected from Peter the Great Bay (northwestern Sea of Japan) contained yellow eggs (2.8 to 3.2 mm in diameter) during July to September, and that spawning occurs in early spring (late March to early April) with larvae in the plankton for two months.

4.3. Potential role in soft-bottom intertidal and subtidal

Cryptacanthodes in the size range collected at PBL occupies its burrows in the lower intertidal and shallow subtidal throughout the year, unlike ephemeral epibenthic residents such as *Fundulus* spp., *Gasterosteus* spp., and *Menidia menidia*. One of us (B. Beal) has observed active wrymouth

burrows at numerous other intertidal soft-bottom sites in eastern Maine (between Blue Hill Bay [44.423654 N; -68.383919 W] and Passamaquoddy Bay) over the past 35 years. Although we surmise the role the wrymouth plays in this benthic community is similar to that of other teleosts, we are unaware of any studies to ascertain its relative importance compared with other predators.

Of 42 fish guts examined, 25 (59.5%) contained the predatory sandworm, *Alitta virens*, and this predator was found in at least one specimen on each sampling date (Table 2). *A. virens* is an intertidal carnivorous annelid [66] that builds permanent burrow that are aggressively defended against conspecifics [67]. Commito & Ambrose [68] and Ambrose [69] define infaunal predators as organisms that live within the sediment and ingest benthic animals. It is unclear whether wrymouth consume benthic infauna while constructing burrows, use burrows to ambush infauna that make temporary forays to the surface to feed or escape their predators (such as *A. virens* [70]), and/or forage widely from their burrows into the upper intertidal or into the subtidal. Therefore, it is not possible to discern at this time whether wrymouths should be considered a fourth infaunal trophic level in soft-bottom communities of eastern Maine (i.e., *C. maculatus*>*A. virens*>*Corophium volutator*>other infauna; see Commito [71]), or included with the suite of shorebirds, crabs, fish, and other epibenthic predators. Regardless, the year-round foraging activities of *C. maculatus* in the lower intertidal and shallow subtidal zone in Maine, as indicated by its gut contents (Table 2), may require adjustments to the trophic interaction model developed for intertidal soft sediment in eastern Maine, USA [68].

5. Conclusion

Much of the ecology and early life-history of *Cryptacanthodes maculatus* are still unknown. Questions remain about its distribution and abundance in the intertidal and shallow subtidal zone, reproductive behavior, habitat for 0-year class and immature individuals, and the role this fish plays in modifying or regulating benthic community dynamics. Based on gut contents from this and other studies, it appears that for at least part of its life-cycle, wrymouth fish likely contribute to trophic linkages between soft-bottom intertidal and shallow subtidal landscapes much like lobsters along rocky shores in southern California [72] and fish in mussel-dominated communities on wave-exposed shores of southern New Zealand [73]. Further investigations should focus on determining seasonal abundance patterns throughout its geographic range, and stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analyses of fish tissue to provide a direct measure of diet as gut contents that contain secondary and tertiary consumers may mask true diet breadth and prey preference.

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Conflict of interest

The authors have no conflict of interest to report.

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Supplementary

Table S1. Presence/absence of infaunal macroinvertebrates per core (A = 0.0182 m²) according to Phylum and Class sampled on 26 May and 8 October 2009 at Perry Boat Landing, Perry, Maine, USA. A total of 27 core samples were taken from each of two tidal heights (Mid and Low tide) on both dates.

	May		October	
	Mid	Low	Mid	Low
	Tide	Tide	Tide	Tide
Annelida				
<u>Oligochaeta</u>				
<i>Tubificoides benedii</i> [Udekem, 1855]	x	x	x	x
<i>Tubificoides</i> spp.	x	x	x	x
<u>Polychaeta</u>				
<i>Alitta succinea</i> [Leuckart, 1847]	x	-	-	-
<i>Alitta virens</i> [M. Sars, 1835]	x	x	x	x
<i>Aricidea (Acmira) catherinae</i> [Laubier, 1967]	x	x	x	x
<i>Aricidea (Strelzovia) suecica</i> [Eliason, 1920]	x	-	x	x
<i>Bipalponephtys neotena</i> [Noyes, 1980]	x	x	x	x
<i>Capitella capitata</i> [Fabricius, 1780]	x	-	-	-
<i>Eteone longa</i> [Fabricius, 1780]	x	x	x	x
<i>Eteone trilineata</i> [Webster & Benedict, 1887]	-	-	x	x
<i>Eudorella truncatula</i> [Bate, 1856]	x	x	x	x
<i>Hartmania moorei</i> [Pettibone, 1955]	-	-	-	x
<i>Harmothoe extenuata</i> [Grube, 1840]	-	-	-	x
<i>Hediste diversicolor</i> [O.F. Müller, 1776]	x	x	x	x
<i>Hypereteone heteropoda</i> [Hartman, 1951]	-	x	-	-
<i>Leitoscoloplos fragilis</i> [Verrill, 1873]	-	x	-	x
<i>Leitoscoloplos robustus</i> [Verrill, 1873]	-	x	-	x
<i>Lumbrineris latreilli</i> [Audouin & Milne Edwards, 1834]	x	x	x	x
<i>Mediomastus ambiseta</i> [Hartman, 1947]	-	x	-	x
<i>Neoamphitrite Johnstoni</i> [Dalyell, 1853]	-	x	-	-
<i>Nephtys caeca</i> [Fabricius, 1780]	-	-	x	-
<i>Nephtys ciliata</i> [Müller, 1776]	x	x	-	x
<i>Nephtys incisa</i> [Malmgren, 1865]	x	-	x	x
<i>Ninoe nigripes</i> [Verrill, 1873]	x	-	x	x
<i>Ophelina acuminata</i> [Örstead, 1843]	x	x	x	x
<i>Parexogone hebes</i> [Webster & Benedict, 1884]	x	x	x	x
<i>Polycirrus eximius</i> [Leidy, 1855]	x	x	x	x
<i>Polycirrus phosphoreus</i> [Verrill, 1880]	x	x	-	x
<i>Polydora cornuta</i> [Bosc, 1802]	x	x	x	x
<i>Protodorvillea kefersteini</i> [McIntosh, 1869]	-	-	-	x
<i>Pygospio elegans</i> [Claparède, 1863]	-	x	x	-
<i>Scoloplos acutus</i> [Verrill, 1873]	-	x	-	-

<i>Sphaerodoropsis minuta</i> [Webster & Benedict, 1867]	-	-	X	X
<i>Terebellides stroemii</i> [Sars, 1835]	-	X	-	-
<i>Tharyx acutus</i> [Webster & Benedict, 1887]	X	X	X	X
Arthropoda				
<u>Malacostraca</u>				
<i>Ampelisca abdita</i> [Mills, 1964]	X	X	X	X
<i>Ampelisca vadorum</i> [Mills, 1963]	X	X	-	-
<i>Anonyx lilljeborgii</i> [Boeck, 1871]	-	-	X	X
<i>Corophium volutator</i> [Pallas, 1766]	X	X	X	X
<i>Crangon septemspinosa</i> [Say, 1818]	X	X	X	-
<i>Crassikorophium crassicorne</i> [Bruzelius, 1859]	-	X	-	-
<i>Edotia triloba</i> [Say, 1818]	X	X	X	-
<i>Harpinia propinqua</i> [Sars, 1891]	X	X	-	-
<i>Jaera (Jaera) albifrons</i> [Leach, 1814]	X	-	-	-
<i>Leptocheirus pinguis</i> [Stimpson, 1853]	X	X	X	X
<i>Monocorophium acherusicum</i> [Costa, 1853]	-	X	-	-
<i>Mysis stenolepis</i> [S.I. Smith, 1873]	-	X	-	-
<i>Orchomene pinguis</i> [Boeck, 1861]	X	X	-	-
<i>Oxyurostylis smithi</i> [Calman, 1912]	X	X	X	-
<i>Phoxocephalus holbolli</i> [Krøyer, 1842]	X	X	X	X
<i>Pontoporeia femorata</i> [Krøyer, 1842]	X	X	X	X
Chordata				
<u>Actinopterygii</u>				
<i>Myoxocephalus aenaeus</i> [Mitchill, 1814]	-	X	-	-
Echinodermata				
<u>Holothuroidea</u>				
<i>Molpadia oolitica</i> [Pourtalès, 1851]	X	-	-	-
Hemichordata				
<u>Enteropneusta</u>				
<i>Saccoglossus kowalevskii</i> [Agassiz, 1873]	X	X	X	-
Mollusca				
<u>Bivalvia</u>				
<i>Gemma gemma</i> [Totten, 1834]	X	X	-	-
<i>Macoma balthica</i> [L., 1758]	-	-	X	X
<i>Musculus discors</i> [L., 1767]	-	X	-	-
<i>Mya arenaria</i> [L., 1758]	X	X	X	X
<i>Nucula proxima</i> [Say, 1822]	-	X	-	-
<u>Gastropoda</u>				
<i>Ecrobia truncata</i> [Vanatta, 1924]	X	X	X	X
<i>Littorina littorea</i> [L., 1758]	-	-	X	-
<i>Onoba aculeus</i> [Gould, 1841]	-	-	X	-
<i>Retusa obtusa</i> [Montagu, 1803]	X	X	X	X