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Voracious planktonic hydroids: unexpected predatory impact on a coastal marine ecosystem

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Abstract—Hydroids are typically attached, benthic cnidarians that feed on a variety of small prey. During sampling on Georges Bank in spring 1994, we found huge numbers of hydroids suspended in the plankton. They fed on young stages of copepods that are an important prey for fish, as well as on young fish themselves. Two independent methods were used to estimate feeding rates of the hydroids; both indicate that the hydroids are capable of consuming from 50% to over 100% of the daily production of young copepods. These results suggest that hydroids can have a profound effect on the population dynamics of zooplankton and young fish on Georges Bank. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

The life history of marine hydrozoans (Phylum Cnidaria) is typically an alternation between a sessile hydroid phase and a motile medusa. The hydroids form colonies attached to seaweed, rocks or other organisms, and their feeding polyps (hydranths) prey on small organisms, eggs and detrital matter. The medusae are usually released to feed and disperse in the plankton (Hyman, 1940).

We report observations from Georges Bank on the occurrence of suspended colony fragments of the hydroid *Clytia gracilis*, a species that normally grows attached to seagrasses or on sandy bottoms. Floating hydroids of *Clytia* spp. are known from several locations (Cornelius, 1982); they are evidently torn loose from their benthic habitat and suspended in the water column, presumably by storm turbulence. Although large numbers of planktonic hydroids have been reported on Georges Bank since the early 1900s (Fraser, 1915), their numbers have never been quantified nor their role in the plankton community

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assessed. Our recent findings suggest that their presence has important implications for other zooplankton and fish in the pelagic ecosystem.

METHODS

The Global Ocean Ecosystems Dynamics (GLOBEC) research program for the Northwest Atlantic Ocean is focused on the population dynamics of several key species of zooplankton and fish, and the biological and physical processes that influence them. As part of this program, we sampled the plankton over the shallow (*ca* 45 m), well-mixed region of Georges Bank (41°10′N, 67°35′W) in May 1994. A 1.0 m^2 multiple opening and closing net system (Wiebe *et al.*, 1985) was used to make duplicate stratified tows (approximately 5 m strata from 0–45 m) near noon and midnight. Additionally, we made direct observations of the composition of the plankton by SCUBA diving.

We used two approaches to estimate feeding rates of the hydroids. First, we examined the gut contents of hydroids collected in nets and with a pump sampling system for remains of eggs or nauplii. Digestion times for these prey were determined by observation in laboratory feeding trials.

The second approach used colony fragments collected from nets for shipboard experiments to determine feeding rates on eggs of the copepods *Calanus finmarchicus* and *Temora* sp., species that are abundant and important prey items for young fishes on Georges Bank (Kane, 1984). Hydroid colonies were introduced into replicate 1-l jars containing 100 or 150 copepod eggs, and maintained on a rotating plankton wheel at ambient sea surface temperature for 12 h. Feeding rates, expressed as prey per hydranth per hour, were

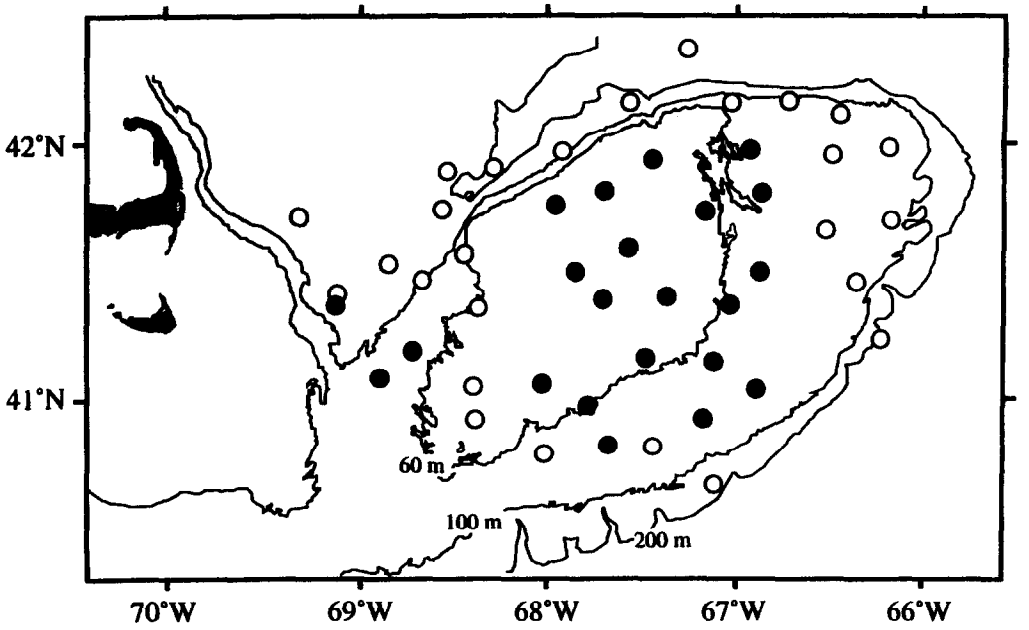

Fig. 1. Areal distribution of suspended *C. gracilis* on Georges Bank. Solid circles indicate stations where hydroids were found; empty circles are negative stations. Silhouette indicates Massachusetts coast.

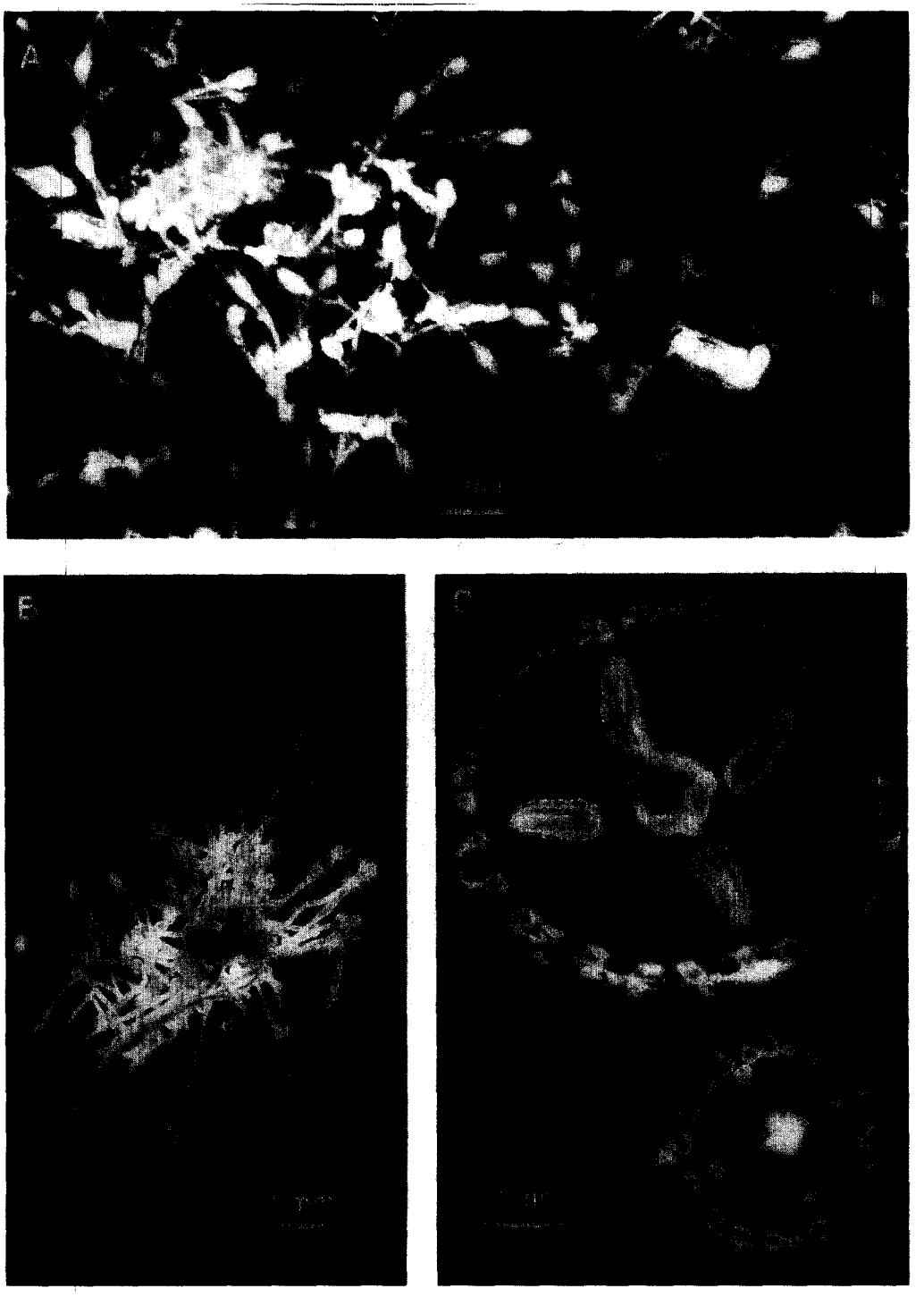

Fig. 2. *Clytia gracilis* (A) hydroid colony fragments from plankton collections; (B) suspended hydroid colony grown in culture; (C) young and mature medusae produced in culture. Scale bar = 1 mm.

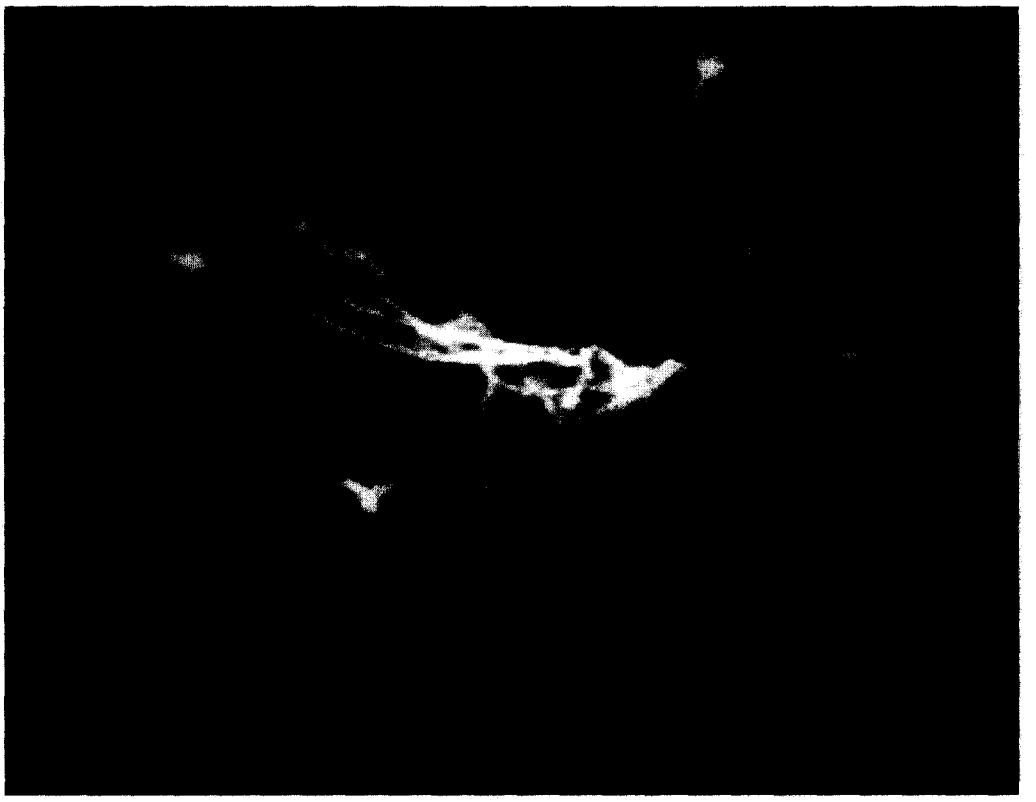

Fig. 3. Larval cod (5 mm long) caught by a hydroid in the laboratory.

calculated from the number of eggs missing at the end of the experiment. Replicate control jars (without hydroids) were run to account for loss of eggs for other reasons. We also established the colonies in laboratory cultures on shore, and used these hydroids in additional experiments to measure feeding rates on the nauplius larvae of *C. finmarchicus*, and on eggs and larvae of the cod (*Gadus morhua*). These experiments were also conducted in 1-l jars on a rotating plankton wheel held in a coldroom at 17°C, but lower densities of nauplii (10–50 l^{-1}) or cod larvae (10 l^{-1}) were used.

RESULTS AND DISCUSSION

We found suspended fragments of hydroid colonies (principally *C. gracilis*, but including other species of *Clytia* and *Obelia*) to be the overwhelmingly dominant component of the net zooplankton. Additional samples taken during a survey of the entire Bank showed that the colonies were widely distributed over the central plateau from May to June 1994 (Fig. 1). Colony fragments consisted of 2–5 polyps (hydranths) each. The maximum observed abundance of 25 000 hydranths m^{-3} occurred near the bottom, but hydroids also dominated the uppermost layers at densities up to 10 000 m^{-3}. Observation by SCUBA divers and by microscopy confirmed that the hydranths were extended and active (Fig. 2(A)), appearing to be healthy and functioning normally as ambush predators in the water column.

Fragments of *Clytia* colonies grew readily in culture on a diet of *Artemia* nauplii, forming new colonies by asexual reproduction and fragmentation, and also producing the sexual medusa stage (Fig. 2(C)), which matured and produced planula larvae. If allowed to settle in a dish, the colony fragments attached to the substrate and assumed their normal benthic form, but if kept in suspension they grew to a radially symmetrical stellate shape (Fig. 2(B)).

Observation of live hydroids in the laboratory showed that they were capable of catching and eating yolk-sac stage larval cod (Fig. 3) as well as the eggs, nauplii, and copepodite stages of copepods (mainly *C. finmarchicus*), which are the main food of larval cod. Early stage nauplii of *Calanus* were digested beyond recognition in less than 15 min, but *Calanus* eggs required about 33 h. The medusae ate cod eggs and larvae also, but were unable to digest the eggs. Examination of gut contents of freshly-collected hydranths (from pump samples) indicated that about 15% of them contained copepod eggs. These data were used to estimate an *in situ* ingestion rate of 0.11 eggs $hydranth^{-1}$ day^{-1}.

The results of shipboard and laboratory feeding experiments on copepod eggs and nauplii and cod larvae showed that feeding rate ranged from about 0.01 to 0.96 prey $hydranth^{-1}$ h^{-1} over a 15-fold range in prey density (Fig. 4). The mean clearance rate calculated for hydroids feeding on copepod eggs was 3.6 ml $hydranth^{-1}$ h^{-1} (s.d. = 3.0, n = 18), while for copepod nauplii it was 1.9 ml $hydranth^{-1}$ h^{-1} (s.d. = 1.1, n = 18).

The total abundance of copepod nauplii sampled at the same site one month later was about 10 000 m^{-3}; eggs of the principal copepod species were produced at a rate of 2300 m^{-3} day^{-1}. Larval cod were far less abundant, fewer than 10 fish per 1000 m^3. Using these values we can make a conservative estimate of predation impact based on *in situ* feeding rates on eggs (0.11 eggs $hydranth^{-1}$ day^{-1}) and experimental results for nauplii at a prey density of 10 000 m^{-3} (0.24 nauplii $hydranth^{-1}$ day^{-1}). Hydroids at a density of 10 000 hydranths m^{-3} would consume nearly half the daily production of copepod eggs and about a quarter of the stock of nauplii per day. Direct predation on the sparse cod larvae might also be considerable at these high densities of hydroids.

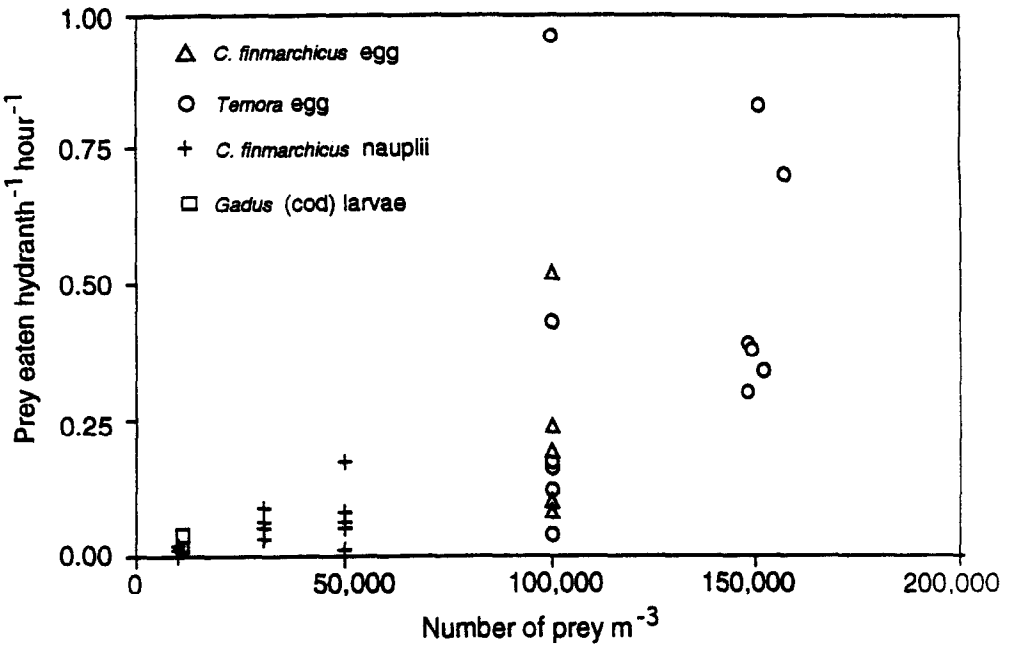

Fig. 4. Results of laboratory feeding experiments with *C. gracilis* hydroids consuming eggs and nauplii of copepods and larvae of cod.

Food availability and predation mortality are both important factors in the early life history of marine fishes (Rothschild, 1986; Houde, 1987), probably regulating the recruitment of commercially important stocks such as cod and haddock (Fogarty *et al.*, 1987). These planktonic hydroids have not previously been recognized as important predators, but our results show how they may seriously affect young fish and other populations of marine organisms directly as predators and indirectly as competitors for copepod prey.

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