

Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA

Jason S. Link^{1,*}, Michael D. Ford²

¹Food Web Dynamics Program, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, Massachusetts 02543, USA

²NOAA/NESDIS/National Oceanographic Data Center, SSMCIII E/OC1 Room 4716, 1315 East-West Highway, Silver Spring, Maryland 20707, USA

ABSTRACT: Changes in the prey composition of the stomachs of opportunistic-feeding fishes can provide information on various ocean-ecosystem dynamics. From 1981 to 2000, stomach samples of the spiny dogfish *Squalus acanthias* showed a major increase in the overall occurrence (and hence implied abundance) of Ctenophora, gelatinous zooplankton that range throughout the ecosystem. There have been a few such major increases in ctenophores in enclosed (e.g. Caspian Sea) and semi-enclosed (e.g. Mediterranean Sea) ecosystems, with concomitant significant effects on those ecosystems and the productivity of their fishery resources. We show the first such increases in ctenophores in an open ecosystem, persistent over 2 decades, with implications for the productivity of the fishery resources in any large marine ecosystem.

KEY WORDS: Gelatinous zooplankton · Large marine ecosystem · Global-scale perturbation · Ctenophore abundance · Spiny dogfish · Regime shift

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INTRODUCTION

The world's oceans are experiencing a wide range of perturbations on an unprecedented scale, including atmospheric and water mass warming (e.g. Walther et al. 2002, Hughes et al. 2003), eutrophication (e.g. Jackson et al. 2001, Deegan 2002), and overfishing (e.g. Pauly et al. 1998, Jackson et al. 2001). Yet it is often difficult to detect overall systemic responses indicative of and sensitive to these perturbations at scales meaningful to large marine ecosystems. One potentially useful indicator of major marine ecosystem alteration is changes in the abundance of gelatinous zooplankton (Mills 2001).

Instances of gelatinous zooplankton blooms are extant for a wide range of marine ecosystems. Both short-term, seasonal increases ('blooms' or 'outbreaks') and long-term, multiyear increases of Ctenophora have been documented for enclosed (e.g. Black Sea, Caspian Sea, Sea of Azov, Sea of Marmara) and relatively enclosed/semi-open (e.g. Adriatic Sea, Baltic Sea, Gulf of Mexico, Bering Sea, Mediterranean Sea)

marine ecosystems, (Purcell et al. 2001, Shiganova et al. 2001, Brodeur et al. 2002, Gucu 2002, Bilio & Niermann 2004). These increases have been variously attributed to eutrophication, water mass warming, and overfishing (Purcell et al. 2001, Shiganova et al. 2001, Sullivan et al. 2001, Brodeur et al. 2002, Gucu 2002, Weisse et al. 2002, Purcell 2005). These increases can also have significant, negative, ecosystem-wide impacts (e.g. Arai 1988, Mills 1995, Purcell & Arai 2001).

However, sampling gelatinous zooplankton remains a major challenge for biological oceanography (Hamner et al. 1975, Weisse et al. 2002). One way to overcome sampling difficulties for gelatinous organisms is to use a low-tech, *in situ* sampling device. Using fish stomachs as integrative samplers has become increasingly widespread for obtaining basic but vital information on difficult-to-sample marine organisms (Fahrig et al. 1993, Frid & Hall 1999, Link 2004).

The objectives of our study were to evaluate potential changes in ctenophore abundance and distribution while describing an approach that may have broad application for sampling the relative abundance of

these types of organisms. We used stomach contents of the spiny dogfish *Squalus acanthias*, a known omnivore in the NE US shelf ecosystem, to ascertain the frequency of occurrence of common gelatinous zooplankton, Ctenophora. We then used these occurrences to serve as a potential indicator of the relative abundance of these gelatinous organisms in this large marine ecosystem.

MATERIALS AND METHODS

The broad-scale, long-term sampling program of stomach contents of fishes from the NE US shelf ecosystem serves directly to identify changes in fish diets and indirectly to identify changes in the underlying ecosystem (Link & Almeida 2000, Link et al. 2002a, Link 2004). The standard Northeast Fisheries Science Center (NEFSC) bottom trawl survey program has been conducted annually since 1963 (Azarovitz 1981, NEFC 1988). During these surveys, food habits data are collected from a variety of species. These multi-species surveys are designed to monitor trends in abundance and distribution and to provide samples to study the ecology of the large number of fish and invertebrate species inhabiting the region. These broad-scale trawl surveys cover continental shelf waters from Cape Hatteras, North Carolina to Nova Scotia (approximately 290 000 km²). All 4 seasons are sampled, but the major focus has been in spring (March to May) and fall (September to November), with winter and summer surveyed more sporadically. The surveys generally utilize a No. 36 Yankee (or similar) bottom trawl towed at approximately 6.5 km h⁻¹ for 30 min at each station. Trawl stations are selected using a stratified random design. Within each depth-region stratum, stations are assigned randomly, and the number of stations allotted to a stratum are in proportion to its area. Station allotments are approximately 1 station 690 km⁻². The surveys are conducted at depths from approximately 27 to 366 m; however, greater depths are occasionally sampled in the canyons along the continental shelf break. Once onboard, fish are sorted to species, weighed (to the nearest 0.1 kg) and measured (to the nearest cm), sex and maturity are determined, and subsamples of key species are eviscerated for feeding ecology studies. Azarovitz (1981) and NEFC (1988) provide a more detailed description of the survey program.

Although the program started in 1973, we focused our study of spiny dogfish stomachs ($n = 43\,489$) from 1981 to 2000 throughout the entire range of the NMFS NE Shelf surveys (i.e. from Cape Hatteras, North Carolina to Nova Scotia). Full details of the food habits sampling and data are given in Link & Almeida (2000) and

are only summarized here with particular respect to spiny dogfish. We omitted earlier years of the food habits program to mitigate any concerns over slight differences in sampling methodology. In each year of this study, at least 1000 spiny dogfish stomachs were sampled; usually the number was over 2000. During the period of the study, spiny dogfish stomachs were examined and prey identified on board ship immediately after the catch had been sorted on deck. Thus, concerns over the degradation of any gelatinous zooplankton due to the effects of preservation in formalin or ethanol (Purcell 1988) or rapid digestion (Arai et al. 2003) are largely unmerited. Data on total stomach volume (± 0.1 cm³), prey composition (%), numbers and lengths were collected on board ship. In addition, a conversion from volumetric measurement of prey (± 0.1 cm³) to mass (g) was executed.

Ctenophora were readily identifiable in the stomachs of spiny dogfish by macroscopic inspection at sea, by their obvious firm-gelatin constitution, small and clear ball-like shape, uniquely (relative to any other spiny dogfish prey) colored, pinkish-gray masses, and obvious 'comb' structures. Even after partial digestion, Ctenophora in spiny dogfish stomachs were identifiable, particularly the ctenes. It appears that spiny dogfish do not masticate Ctenophora, but rather ingest these as whole prey items. Compared to direct methods of sampling gelatinous zooplankton in the marine environment (e.g. nets), our stomach sampling methods largely eliminated concerns over specimens breaking apart and becoming unidentifiable and/or indistinguishable (Hamner et al. 1975, Bailey et al. 1994, Weisse et al. 2002).

We used frequency of occurrence instead of diet composition as an index of Ctenophora abundance because (1) diet composition is much more dynamic and liable to be influenced by predator density and alternate prey than frequency of occurrence; (2) the evidence from other studies suggests that this ecosystem is a donor-controlled, bottom-up driven ecosystem (Fogarty & Murawski 1998, Link & Brodziak 2002), and any occurrence of a prey item in the stomach of a predator is ultimately indicative of its abundance in the ecosystem; and (3) frequency of occurrence is less biased than other estimators and simply represents how often a prey item was eaten or 'sampled' relative to the number of stomachs examined (Link 2004).

Spiny dogfish are known omnivores and opportunistic pelagic feeders, which feed as they swim through the water column. Thus, heightened selectivity for or against ctenophore prey should not be a major consideration. The concern of prey selectivity is further mitigated by the consistent percent diet composition of Ctenophora in dogfish and the known

opportunistic feeding nature of this fish (*sensu* Fahrig et al. 1993, Frid & Hall 1999, Link et al. 2002b, Link 2004). To validate the relative consistency that Ctenophora comprise of spiny dogfish diets, we present percent diet composition (by weight) of Ctenophora and the average amount (g) of Ctenophora consumed.

Additionally, we sought corroborating evidence for ctenophore increases, but although we examined some NW Atlantic regional zooplankton databases (NESFC unpubl. data), the data were inconclusive given the caveats of the sample processing protocols. The protocols did not specifically target ctenophores or other gelatinous zooplankton nor treat the processing of such organisms consistently over time.

Since we were looking for changes in ctenophore density distribution and overall abundance over the study period (i.e. 1981 to 2000), geo-referenced locations of tows that contained ctenophore-eating spiny dogfish were plotted. These were done in 5 yr blocks to smooth out interannual variations. This allowed us to evaluate the range and extent of ctenophore occurrence as it changed across the decades. We did not plot occurrences of stations where we caught dogfish, nor where we examined dogfish stomachs that did not contain Ctenophora, since by so doing we would have obscured any patterns in Ctenophora occurrence. Although spiny dogfish abundance increased over the period of the study (NEFSC 1998), the range, distribution and sampling of dogfish, and particularly the sampling of their stomachs, remained consistent (Link & Almeida 2000).

RESULTS

The frequency of occurrence of Ctenophora has increased in the NE US shelf ecosystem by 2 to 8 times since the early 1980s (Fig. 1). This increase has persisted; it is more than a transient, localized, bloom-like phenomenon. That the change has occurred and been sustained over 2 decades likely indicates major changes in the structure and function of this ecosystem (*sensu* Fogarty & Murawski 1998, Link & Brodziak 2002, Link et al. 2002a).

There was no significant trend in the percent composition of Ctenophora in spiny dogfish stomachs (Fig. 2), which varied between 5 and 15%, with a long-term average of 11%. There was also no significant trend in

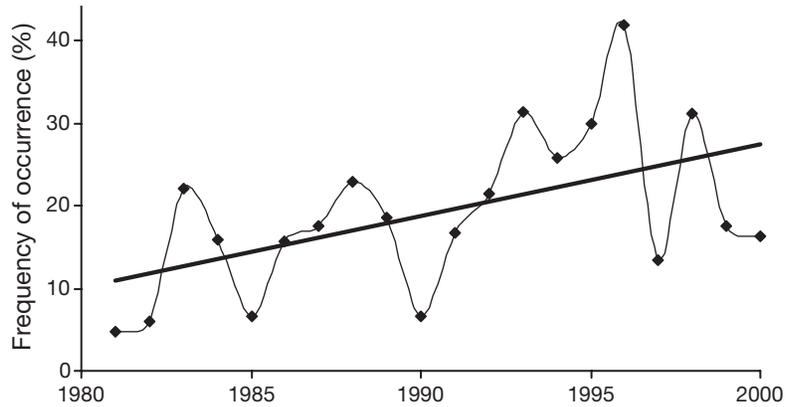


Fig. 1. Percent frequency of occurrence of Ctenophora in spiny dogfish *Squalus acanthias* stomachs from 1981 to 2000. Regression line shown; trend is significant (F -test, $p < 0.001$, $r^2 = 0.35$)

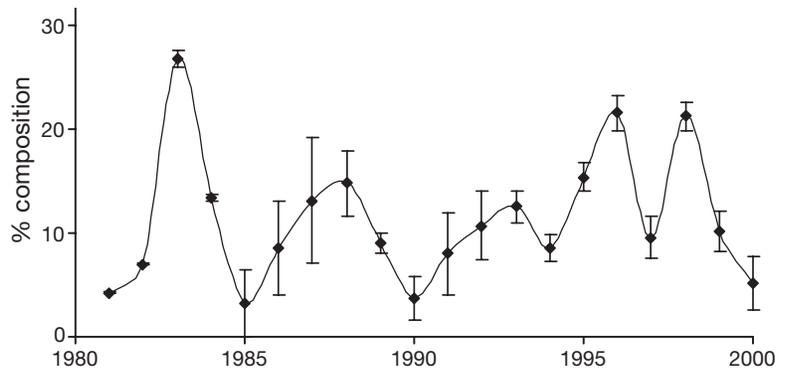


Fig. 2. Mean \pm SE percent diet composition (by weight; g) of Ctenophora in spiny dogfish *Squalus acanthias* stomachs. No significant trend was observed over the study period

the amount of ctenophores consumed by spiny dogfish over the time series (Fig. 3), with a long-term average of 2.1 g, varying between 0.5 and 5 g. This indicates that feeding by spiny dogfish on Ctenophora is a common, routine, non-selective, maintenance-feeding type of process that is primarily dependent upon ambient abundance of Ctenophora, and in effect depends on the spiny dogfish encountering ctenophores.

The increase in Ctenophora has also been widespread, exhibiting the classical expansion of range over time when a population continues to increase (Fig. 4). Most occurrences of Ctenophora have been in the Southern New England and Georges Bank regions (Fig. 4). However, there was a clear expansion both north into the Gulf of Maine and south into the Mid-Atlantic over the period of the study.

Taking into consideration the distribution of these occurrences, the stomach contents identified as Ctenophora could have been *Mnemiopsis leidy*, *Pleurobrachia pileus* or *Bolinopsis infundibulum*. The lobate ctenophore *M. leidy* has been observed from Georges Bank/Cape Cod to the southern extent of our study

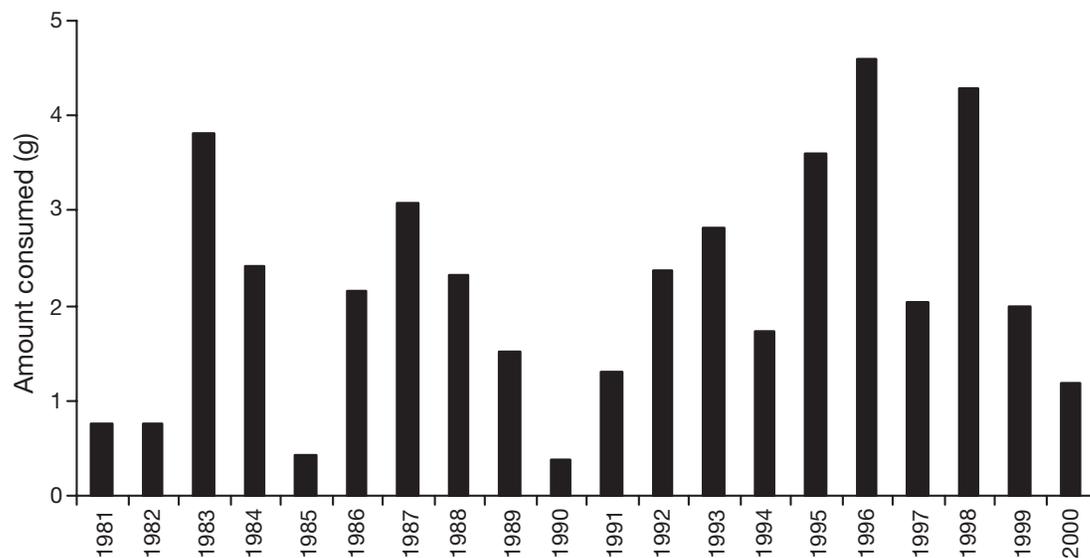


Fig. 3. Average amount of Ctenophore consumed by spiny dogfish *Squalus acanthias*. No significant trend was observed over the study period

region (e.g. Kremer 1994, Purcell et al. 2001). *P. pileus*, a tentaculate ctenophore, has been observed in the Gulf of Maine and on the Scotian Shelf (Frank 1986, Mills 1995), suggesting that this species is common in more northern waters. *B. infundibulum* is a lobate ctenophore found in coastal waters from New England to Labrador, and extending as far as the Arctic and Baltic Seas (Bailey et al. 1994). It is possible that one, a combination, or all 3 of these species were present in the stomach contents of *Squalus acanthias* in our study, but our sampling protocol precluded definitive identification at the species level.

DISCUSSION

Our observations of major increases in Ctenophora occurrence, and hence implied abundance, at the scale of an entire large marine ecosystem (i.e. major portions of ocean basins) and over such a long period are significant. We attribute this persistent and widespread increase in Ctenophora in the NE US shelf ecosystem to a combination of local warming of water masses (Sullivan et al. 2001, Mountain 2003) and overfishing (Fogarty & Murawski 1998, Link et al. 2002a). Such an increase at the scale of an entire large marine ecosystem and over more than 2 decades has not been previously documented. It coincides with, to some extent contributes to, and may be a useful indicator of major changes in the structure and function (e.g. energy flow) of this ecosystem (Fogarty & Murawski 1998, Link & Brodziak 2002).

Other hypotheses could explain the patterns observed in the data. For example, an overall change in

the diet of spiny dogfish *Squalus acanthias* arising from changes in the distribution or relative abundance of other prey, changes in *S. acanthias* physiology such that the total amount of food consumed changed, or changes in *S. acanthias* behavior (either foraging or otherwise) are all possible feeding-related explanations. Relative to the 'sampling device', changes in the sampling protocol, in the frequency of sampling *S. acanthias* stomachs, or in *S. acanthias* distribution or catchability might also explain the observed patterns. These and similar considerations are all possible reasons for an increase in the frequency of occurrence of Ctenophora in *S. acanthias* stomachs. Of these, we can rule out major changes in sampling protocol (Link & Almeida 2000), catchability of spiny dogfish in the surveys (Azarovitz 1981, NEFSC 1998), sampling frequency of stomachs (Link & Almeida 2000) and changes in the distribution of *S. acanthias* (NEFSC 1998, unpubl. data).

Other studies have shown that the diet composition of spiny dogfish has changed over time (Link et al. 2002b, Link & Brodziak 2002). However, most changes in their diet have not concerned major functional groups of prey, but rather species compositions within those groups (e.g. varying species of small pelagic fishes) in response to the relative abundance of such prey in the environment. However, the studies of Link et al. (2002b) and Link & Brodziak (2002) and the present study show that the diet composition of Ctenophora in the spiny dogfish has remained consistent, with no significant trends, and generally averaging between 5 and 15%. Certainly, changes in alternate prey could influence spiny dogfish feeding, but again, ctenophores comprised a relatively consistent amount

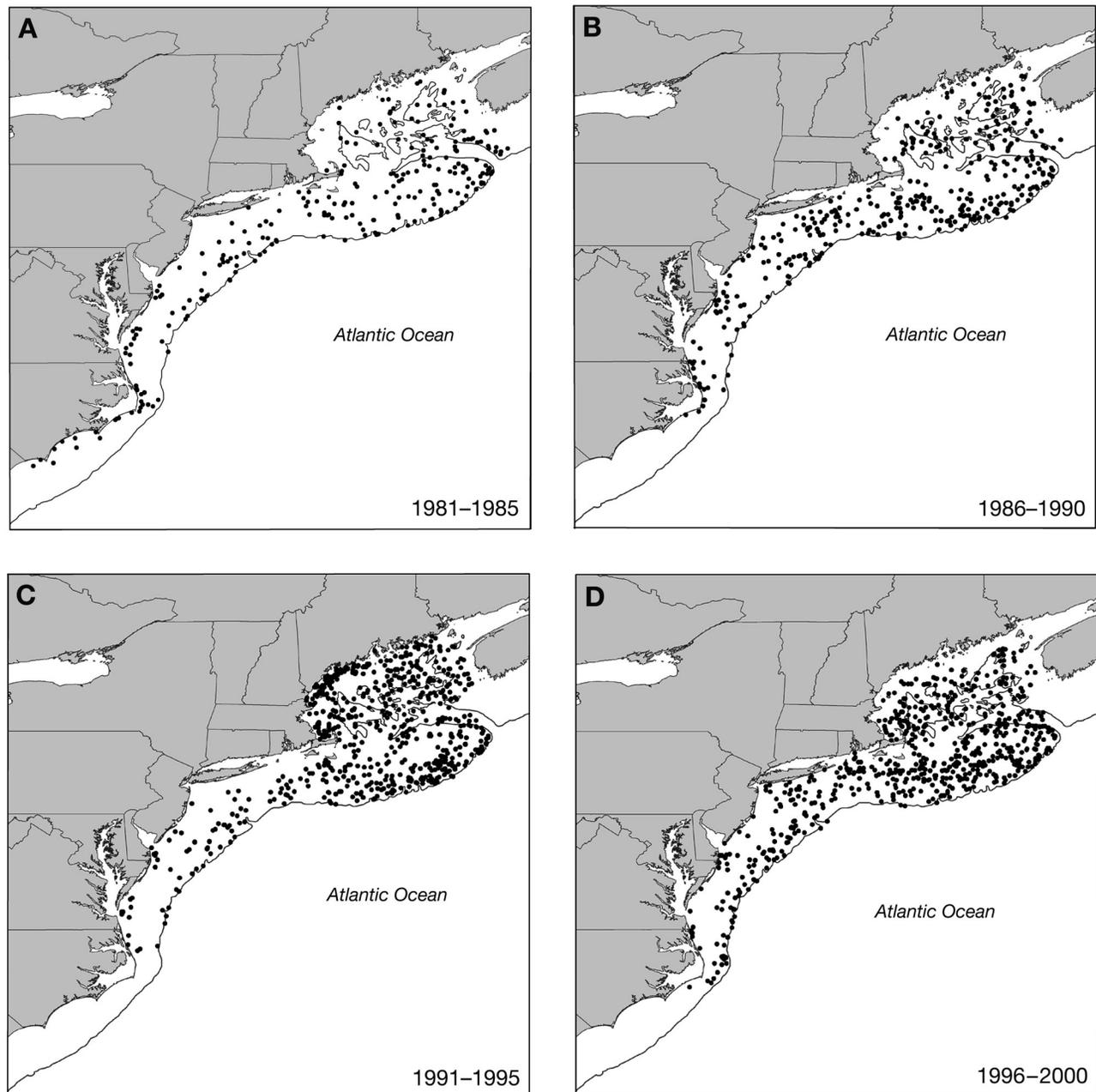


Fig. 4. Location of stations at which spiny dogfish *Squalus acanthias* stomachs contained Ctenophora. (A) to (D) illustrate 5 yr intervals; 200 m isobath is shown. Area plotted is from 46° 20' to 32° 00' N latitude and 64° 40' to 79° 00' W longitude

of the diet throughout the study period (Link et al. 2002b, Link & Brodziak 2002). Additionally, there was no clear trend in the amount of ctenophores eaten by spiny dogfish, suggesting a relative constancy in the factors that determine the amount of Ctenophora they consume.

Although we believe that our observations strongly indicate that ctenophores have indeed increased in abundance, without direct sampling we cannot be absolutely sure. Although other explanations con-

nected with changes related to spiny dogfish feeding or 'ctenophore sampler' protocols are possible, none of them provide a convincing explanation for the observed patterns. Of all the possible alternatives, the explanation of increased Ctenophora abundance is the most logical, given the available evidence.

Although instances of increased ctenophore abundance have previously been reported for partially or fully enclosed systems (Purcell et al. 2001, Shiganova et al. 2001, Brodeur et al. 2002, Gucu 2002, Weisse et

al. 2002, Bilio & Niermann 2004), our study of the open system of the NE US shelf ecosystem suggests that virtually all the world's marine ecosystems are vulnerable to such increases in ctenophore abundance. Given the difficulty of sampling gelatinous zooplankton (Hamner et al. 1975, Weisse et al. 2002), both long-term and short-term increases in ctenophore abundance may already be more common than previously recognized (*sensu* Mills 2001), particularly in response to climate change (Purcell 2005).

The ecological effects of increasing ctenophore abundance can be significant, especially through competition with and predation upon other organisms (Arai 1988, Mills 1995, Purcell & Arai 2001). Increased ctenophore abundance has altered food webs, either directly or indirectly, and in particular via predation by ctenophores on larval and juvenile stages of commercially valuable fish species (Arai 1988, Mills 1995, Purcell & Arai 2001, Purcell et al. 2001, Bilio & Niermann 2004), which has been suspected of hindering recruitment in a wide range of species (Purcell & Arai 2001, Purcell et al. 2001, Bilio & Niermann 2004). A negatively reinforcing feedback loop has been described, whereby overfishing contributes to conditions suitable for increased ctenophore abundance, which in turn contributes to decreased fish recruitment, which contributes to decreased fish stocks, which contributes to overfishing, with the loop then iterating (Mills 1995, Purcell & Arai 2001, Purcell et al. 2001, Weisse et al. 2002, Bilio & Niermann 2004). Other possible effects of increased ctenophore abundance include an increase in the amount of unaccounted-for or difficult-to-sample biomass in a system, declines in future fish yields, increased production of ctenophore predators (which may not be desirable organisms), in addition to further unintended and/or indirect effects that have not yet been detected.

Some scientists have jokingly suggested that continued ocean perturbations may leave us with marine ecosystems populated predominantly by jellyfish (Pauly et al. 1998, *sensu* Jackson et al. 2001, Pauly & Watson 2003); we may be closer to such a situation than we suspect.

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