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REVIEW

Climate effects on formation of jellyfish and ctenophore blooms: a review

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Much speculation and some evidence suggest that jellyfish and ctenophore populations have increased in recent decades. Unfortunately, few past records exist with which to compare current populations, and our knowledge of how environmental factors affect jellyfish population size is meagre. Human enterprise has wrought many changes in the ocean that are hypothesized to favour jellyfish, including eutrophication, reduction of fish stocks, and global warming. In addition to anthropogenic changes, natural climate cycles may affect jellyfish populations. Records of jellyfish and ctenophore abundance that appear to be related to indices of climate variations (temperature, salinity, North Atlantic Oscillation, North Pacific Decadal Oscillation, El Niño Southern Oscillation) are reviewed. In eleven species studied from subtropical, temperate and subarctic environments, warm temperatures were related to large population sizes; three scyphozoan species in the North Sea, and one mesopelagic hydromedusan were exceptions to that trend. One tropical scyphomedusan species was decimated by unusually warm, salty El Niño conditions in Palau. Because climate changes have complex ecosystem-level effects, the proximate causes of jellyfish increases are difficult to deduce. Therefore, the effects of temperature, salinity and prey on asexual production of new medusae from the benthic polyps of scyphomedusae and hydromedusae also are reviewed. Experiments on temperate species show greater and more rapid production of medusae at warmer temperatures. Salinity also had significant effects, and was especially important for estuarine species. Temperature and salinity affect asexual reproduction rates directly through metabolism, and indirectly through prey capture. Ocean warming may shift the distributions, expand the seasonal occurrence, and increase the abundances of temperate-boreal species. Populations living near their thermal maximum may suffer negative consequences of warming.

INTRODUCTION

In recent years, the connections between variations in climate and jellyfish and ctenophore population sizes gradually have been recognized. Jellyfish are known for their sudden blooms of great abundance, which usually are noticed by swimmers or fishers. Few long-term records of jellyfish abundance exist. Most of those records are semi-quantitative, but they have been extremely valuable in correlating changes in jellyfish abundance with climate variations. Because of their short generation times (usually ≤1 year), populations of gelatinous species appear to respond to climate forcing without a time lag (Lynam et al., 2005). Herein, the relatively few examples of long-term records of jellyfish and ctenophore abundance that have been correlated with changes in climate are reviewed. In order to better understand how environmental factors affect population size, results of the few recent experiments on the effects of temperature, salinity and food on asexual reproduction rates of scyphozoans and hydrozoans also are summarized.

Many jellyfish have a two-stage life cycle consisting of the large (millimetres to a metre or more in diameter) swimming medusa stage and the small (millimetres) benthic polyp stage. Medusae reproduce sexually, and the polyps asexually bud more polyps and tiny jellyfish (1–2 mm). In scyphomedusae, the jellyfish are large (>1 cm) and conspicuous, and the polyps undergo transverse fission (strobilation) that produces from one to many new medusae, called ephyrae. In hydromedusae, the jellyfish usually are small (<1 cm) and inconspicuous, and the benthic, usually colonial polyps are called hydroids. In temperate and boreal regions, production of medusae takes place seasonally, often in the spring. The cues that trigger medusa production have not been definitively determined for most species, but apparently include a seasonal progression or combination of environmental changes in temperature, salinity, food, and light, and differ among the various species (reviewed in Spangenberg, 1968; Boero, 1984; Arai, 1992, 1997; Shostak, 1993; Lucas, 2001; Fautin, 2002). The experiments in those reviews were designed to test factors that may initiate medusa production, rather than to determine environmental effects on jellyfish population size.

The life history of ctenophores does not include an asexual benthic stage. Larval ctenophores, produced by the fusion of eggs and sperm in the water, grow directly into adults. Perhaps because of their fragility, little is known about factors that affect their sexual reproduction and population abundances.

The question of whether jellyfish and ctenophore populations are increasing is an important one (Mills, 2001). Linkages to climate variation suggest that jellyfish abundance could rise and fall with ocean basin-wide climate oscillations (El Niño Southern Oscillation, North Atlantic Oscillation, North Pacific Decadal Oscillation) (Anderson & Piatt, 1999; Ottersen et al., 2001; Raskoff, 2001; Austin, 2002; Beaugrand, 2003; Lynam et al., 2004, 2005; Purcell & Decker, 2005). Overlaid on natural climate variation, however, is the potential effect of progressive global warming, which indicates an average warming of 0.31°C in the surface 300 m of the world ocean since the mid-1950s (Levitus et al., 2000). This review will show that the abundances of many jellyfish and ctenophore species may increase in warm conditions. Global warming could result in expanded temporal and spatial distributions and larger populations of jellyfish and ctenophores.

Increases in jellyfish and ctenophore populations generally would be considered to be detrimental to human enterprise, except for the rhizostome scyphomedusan species used as food (Omori & Nakano, 2001). Jellyfish and ctenophores are important consumers of ichthyoplankton and zooplankton, and therefore are both predators and potential competitors of fish (reviewed by Purcell & Arai, 2001). They further interfere with fisheries by clogging fishing nets (e.g. Shimomura, 1959; Yasuda, 1988; Graham et al., 2003). Jellyfish interfere with tourism and are medical liabilities for swimmers (Burnett, 2001). Jellyfish also cause power plants to shut down because of clogged seawater intake screens (Matsueda, 1969; Yasuda, 1988; Rajagopal et al., 1989). Because of their negative effects, it is important to understand which environmental factors may cause increases in jellyfish and ctenophore populations.

Correlations between long-term records of jellyfish, ctenophores, and climate

Mnemiopsis leidyi *A. Agassiz ctenophores in Narragansett Bay and the Black Sea*

Mnemiopsis leidyi ctenophores (<8 cm total length) are conspicuously abundant in estuaries and coastal waters of the eastern United States (reviewed in Kremer, 1994). Genetic analysis is consistent with the existence of one species, *M. leidyi*, from New England through the Gulf of Mexico (Bayha, 2005). Records from Narragansett Bay, Rhode Island, in the northern part of its range, mark the dates of first appearance of the ctenophore since 1950, and periodic intensive studies provide more detailed data on ctenophore appearance, abundance, and water temperature (Sullivan et al., 2001). The ctenophores appeared markedly later in the 1950s and 1970s (July) than in the 1980s and 1999 (May–June) (Figure 1). Their peak abundances also were lower in the earlier decades (5–70 ctenophores m^{-3}) than in later years (60.5–350 ctenophores m^{-3}). During 1950–1999, spring water temperatures there increased about 2°C. The warm years were associated with positive North Atlantic Oscillation Indices (NAOI). Thus, warm temperatures were related to a prolonged period of occurrence and increased abundances of *M. leidyi* ctenophores.

Mnemiopsis leidyi became infamous in the late 1980s because after accidental introduction, it proliferated in the Black Sea and contributed to the destruction of fisheries there (Shiganova, 1998, 2005; Anninsky et al., 2005; Gordina et al., 2005). Retrospective analyses suggest that many anthropogenic changes in the Black Sea, including pollution, decreased freshwater inputs due to damming of major rivers, severe eutrophica-

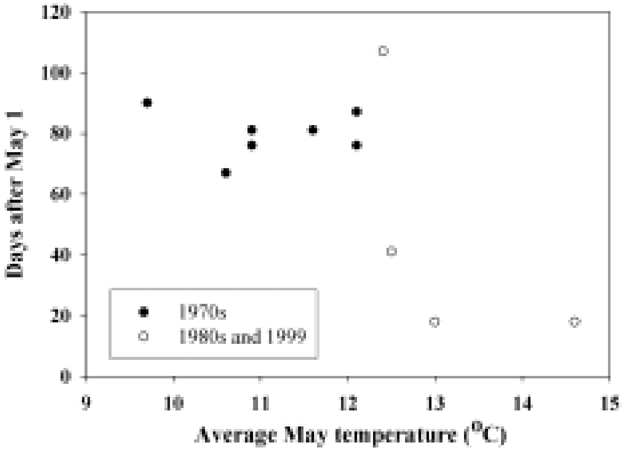

Figure 1. First appearance (Days after May 1) of *Mnemiopsis leidyi* ctenophores versus average May water temperature in Narragansett Bay, Rhode Island in 1970–1999 (drawn from data in Sullivan et al., 2001).

tion and resulting changes in the zooplankton community structure, and over-fishing could have contributed to the collapse of the zooplanktivorous anchovy stock, which probably enabled the ctenophore invader to exploit available zooplankton (e.g. Shiganova, 1998; Purcell et al., 2001; Bilio & Niermann, 2004). Bilio & Niermann (2004) proposed that over-fishing of the anchovy stock coincided with climate-induced changes in the food base, causing collapse of the anchovy population, which allowed proliferation of ctenophores. Oguz (2005a,b) argued that after considering the anthropogenic factors that contributed to the proliferation of *M. leidyi*, climatic factors explain the periods of ctenophore increase and decline in the 1980s and 1990s. The periods 1985–1987 and 1991–1993 had unusually cold winters (1.8°C below normal). The first cold period, shortly after discovery of the ctenophore invasion, may have kept ctenophores from blooming; the second cold period was characterized by low mesozooplankton and anchovy abundance and markedly decreased ctenophore densities following large populations in the summers of a warm period (1989–1991). Negative phases of the NAO and other regional climate indices correspond with warmer temperatures and lower salinities in the Black Sea, conditions that are favourable to the ctenophores.

Both direct and indirect effects of climatic conditions affect ctenophore abundances. Cold winter temperatures (<4°C) prevented over-wintering of *Mnemiopsis leidyi* in the Sea of Azov, and warm spring temperatures in the Black Sea (7.5–8.5°C) and Chesapeake Bay (11.3–14.7°C) correlated with larger ctenophores, which would favour egg production and development of blooms (Purcell et al., 2001). Therefore, the spatial and temporal ranges of the ctenophore are restricted by low temperature, and increase with warming. However, high temperatures may restrict this species, as in the Aegean and Mediterranean Seas, where it has had limited success following its spread from the Black Sea (Purcell et al., 2001). *Mnemiopsis leidyi* is euryhaline, having been collected in salinities from 0.1 to 38 (Purcell et al., 2001; Purcell & Decker, 2005). Low salinity waters provide refuges for *M. leidyi* from predators, such as *Chrysaora quinquecirrha* (Desor) scyphomedusae and *Beroe* sp. ctenophores, and from potential competitors, such as *C. quinquecirrha* and *Aurelia aurita* (Linneaus) scyphomedusae, which cannot tolerate extremely low salinities. Climate conditions that increase zooplankton would benefit ctenophores, as above.

Pelagia noctiluca *(Forskål) scyphomedusae in the Mediterranean and Adriatic Seas*

The longest record of jellyfish abundance is for the scyphomedusan, *Pelagia noctiluca*, in the Mediterranean Sea where it has been reported for over 200 years (Goy et al., 1989). This species is unusual in that it lacks a benthic stage; the medusae develop directly from a planktonic larva. Medusae (<9 cm bell diameter) are widely distributed in subtropical to temperate waters of the Atlantic and Pacific oceans (Kramp, 1961). This species has gained notoriety in the Mediterranean and Adriatic Seas due to periodic blooms that negatively impact swimmers. The consensus of scientific opinion at two international workshops was that the blooms were related to ocean circulation patterns, and that eutrophication and reduction of zooplanktivorous fish (anchovy) may have contributed to prevalence of the medusae (UNEP, 1984, 1991).

Goy et al. (1989) analysed many data sources for the presence and absence of medusae in the

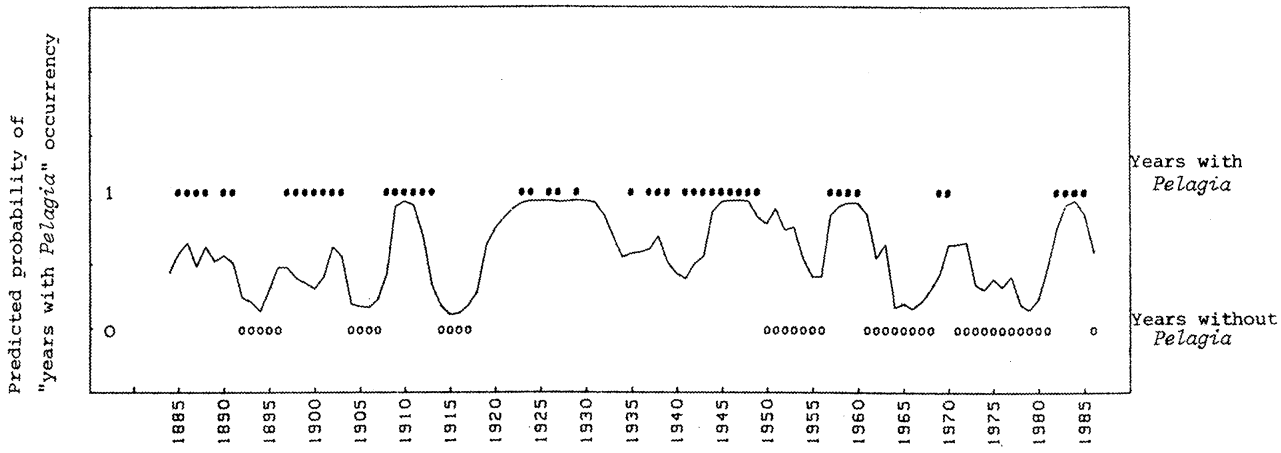

Figure 2. The probability of *Pelagia noctiluca* scyphomedusae occurrence in the Mediterranean Sea as predicted by the model (line), which varies from 0 to 1. Dark circles are years with *Pelagia*, open circles are years without *Pelagia* during 1885–1985 (from Goy et al., 1989).

Mediterranean Sea between 1885 and 1986 (Figure 2), and showed a periodicity of recurrence of about 12 years ($P=0.01$). They then considered 18 meteorological variables and developed a model, which indicated that a lack of rainfall, associated with high temperature and atmospheric pressure from May to August best predicted years of medusa occurrence (Figure 2). They concluded that climate probably correlated with ocean circulation and pelagic production that contributed to the appearance and maintenance of a medusa population.

Similar conclusions were reached for the Adriatic Sea, where *P. noctiluca* bloomed five times during the past two centuries; warm winters, higher ocean temperatures and greater marine water advection from the south provide favourable conditions for influx, retention and reproduction of medusae in the northern Adriatic (reviewed in Purcell et al., 1999b). The conditions that are conducive to medusa bloom formation are temperatures >10°C in winter and <27°C in summer, and salinities of 35–38 (reviewed in Purcell et al., 1999b).

Chrysaora quinquecirrha *(Desor) scyphomedusae in Chesapeake Bay*

Chrysaora quinquecirrha medusae (<18 cm bell diameter) are widely distributed in coastal temperate to subtropical waters in the North and South Atlantic and south-east Asia (Kramp, 1961). This scyphozoan species is unusual in living in low salinity waters, but medusae do not occur at salinities below 5 (Cargo & Schultz, 1967). In years when precipitation in the Chesapeake Bay watershed is great, freshwater input is high, salinities are low, and medusa numbers are low. Daily visual counts of medusae near shore in 1960–1986 were significantly correlated only with January–June freshwater inputs from the major rivers (streamflow; $r^2=0.576$, $P<0.01$); May salinity and temperature were not significant (Figure 3; Cargo & King, 1990). Freshwater affects medusa abundance by determining the salinity, rather than advecting medusae out of the bay. Salinity also can determine the time medusae appear in the mesohaline bay, from May in dry years to August in unusually wet years (Purcell et al., 1999c).

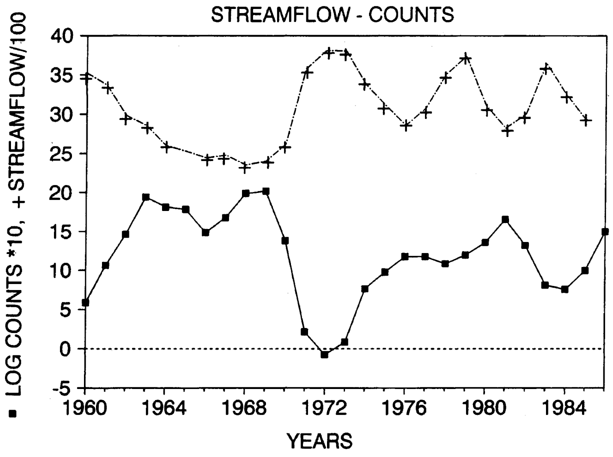

Figure 3. January–June freshwater streamflow ($m^3 s^{-1}$) into Chesapeake Bay (+) and counts of *Chrysaora quinquecirrha* medusae from a pier in mesohaline Chesapeake Bay during July and August in 1960–1986 (■). Values plotted are smoothed by a moving average of three data points (from Cargo & King, 1990).

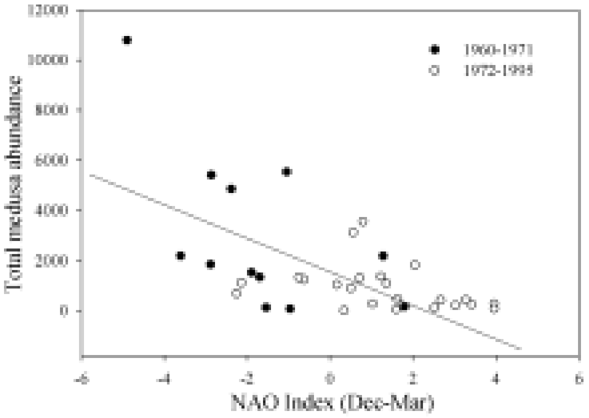

Figure 4. Annual total numbers of *Chrysaora quinquecirrha* scyphomedusae counted daily from a pier in mesohaline Chesapeake Bay versus the North Atlantic Oscillation (NAO) Index during 1960–1995. Filled circles represent years prior to the climate regime shift that followed Hurricane Agnes in 1972 (from Purcell & Decker, 2005). Copyright (2005) by the American Society of Limnology and Oceanography, Inc.

Subsequent analyses showed additional relationships between medusa abundance and climate. Purcell & Decker (2005) used D.G. Cargo's data from 1960–1995 (CBP, 2000) and found that medusa abundance was negatively correlated with the NAOI from the preceding December–March (Figure 4). Medusae were extremely abundant in the 1960s when the NAOI were generally negative. The 1960s were in a cool, dry, regime, which shifted with Hurricane Agnes in 1972 to a warm, wet regime that persists currently (Austin, 2002). The regime shift was accompanied by low medusa numbers and generally positive NAOI. Shorter-term comparisons (1987–1990 and 1995–2000) in mid-Chesapeake Bay showed that high April–May salinities ($P=0.006$), warm July–August temperatures ($P=0.036$), and high spring solar radiation ($P<0.001$) were significantly related to high medusa densities; however, freshwater input ($P=0.23$) and the NAOI ($P=0.18$) were not (Purcell & Decker, 2005).

Conditions that favour frequent occurrence of *C. quinquecirrha* medusae in Chesapeake Bay are salinities of 10–16 and temperatures of 26–30°C in summer (Brown et al., 2002). The preponderance of medusae within those ranges led to development of a model that permits near-real-time prediction (nowcasting) of medusa occurrence (http://coastwatch.noaa.gov/seanettles).

Aurelia *spp. scyphomedusae*

Aurelia spp. are undoubtedly the most studied jellyfish in the world, owing to a cosmopolitan distribution between 70°N and 40°S latitudes, great abundances, and ease of culturing (reviewed in Mills, 2001). They occur over extremely wide ranges of environmental conditions, from Arctic to tropical. Recent molecular studies distinguish distinct genotypes of *Aurelia*, and separate the genus into several species (e.g. Dawson & Jacobs, 2001; Schroth et al., 2002; Dawson, 2003). The native habitat of *Aurelia aurita* Linnaeus is believed to be northern European waters; *Aurelia* sp. 1 appears to have been introduced in several locations around the world, including Japan (Dawson & Jacobs, 2001; Dawson, 2003). Because the species are morphologically similar, *Aurelia* spp. medusae have been called *A. aurita* in many past studies.

Hernoth & Gröndahl (1983, 1985) measured temperature, salinity, solar radiation, and the abundance of *A. aurita* ephyrae and medusae in a Swedish fjord from October to March, 1982 and 1983. Ephyrae were produced mainly in the autumn, overwintered at depth, and moved to surface waters in spring. Strobilation occurred when temperatures and irradiance were decreasing. The numbers of ephyrae in 1983 were 1% of those in 1982, which the authors attributed to predation by a nudibranch; however, temperatures at 5 m depth were 1–2°C cooler in 1983 as well.

Increasing *Aurelia* sp. populations in Japan are associated with problems of the medusae clogging power plant seawater intake screens (Matsueda, 1969; Yasuda, 1988; Matsumura et al., 2005), displacing fish (Uye & Ueta, 2004), and occurring in unusually extensive aggregations in inland waters (Uye et al., 2003; Uye & Ueta, 2004). In the eastern and western Inland Sea of Japan, where winter minimum temperatures have increased about 1.5°C since 1983 to >11°C, a poll of 1152 fishermen with >20 years experience indicated that medusae have become more abundant and have extended their season over the last 20 y (Uye & Ueta, 2004). High abundances of medusae in eutrophic Tokyo Bay co-occur with predominant small *Oithona davisae* Ferrari & Orsi copepods, which are poor food for zooplanktivorous fish (Ishii & Tanaka, 2001).

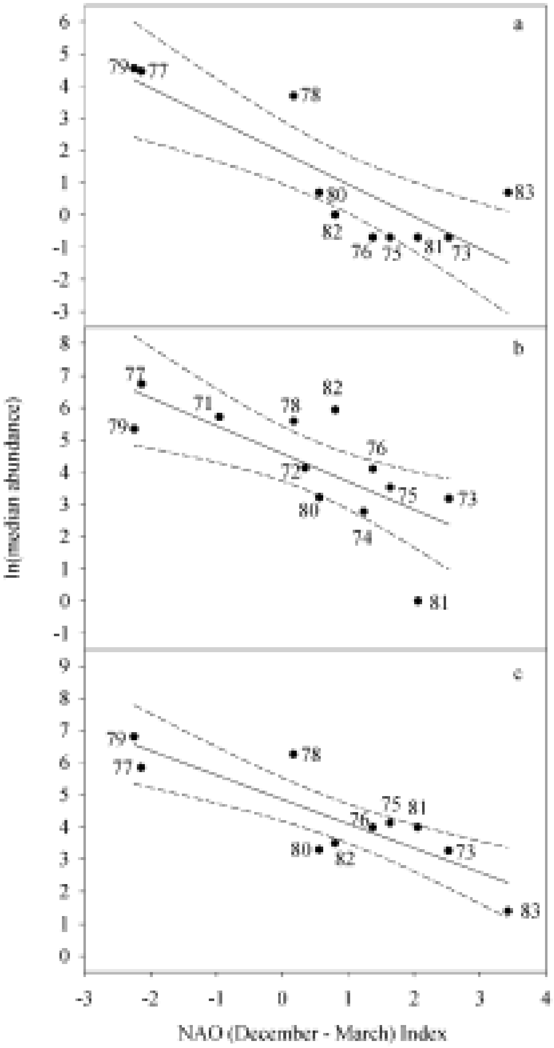

Figure 5. Linear regressions of scyphomedusa abundance against the North Atlantic Oscillation (December–March) Index. Solid line is the model fit; dashed lines are the 95% confidence intervals. (A) *Aurelia aurita* west of northern Denmark; (B) *Aurelia aurita* east of Scotland; (C) *Cyanea lamarckii* west of northern Denmark. Numbers represent years 1971–1986 (from Lynam et al., 2004). Copyright (2004) by the American Society of Limnology and Oceanography, Inc.

Aurelia aurita, Cyanea lamarckii *Péron & Lesueur and* Cyanea capillata *(Linnaeus) scyphomedusae in the North Sea*

Fishery records of bycatch have provided valuable long-term information on jellyfish abundance. Lynam et al. (2004) showed strong inverse correlations of medusa bycatch (median abundance) in June–August from two locations in the North Sea with the preceding December–March NAOI during 1971–1986 for *Aurelia aurita* (west of northern Denmark (WND), r^2=0.70, P=0.003; east of Scotland (EOS), r^2=0.53, P=0.008) and *Cyanea lamarckii* (WND, r^2=0.74, P=0.002) (Figure 5). In a subsequent analysis (Lynam et al., 2005), a negative correlation between the NAOI and maximum abundance of *Cyanea capillata* was also found EOS. The new analysis emphasizes differences by region, where correlations between *A. aurita* and *C. lamarckii* north of Scotland (NOS) and the NAOI were positive instead of negative (as in the south-eastern North Sea, i.e. WND). North of Scotland is in a region where correlations between the NAOI and sea surface temperature (SST) switch from positive (as at WND) to negative. Temperatures and salinities during sampling were not presented in either analysis. A cold event occurred between 1978 and 1982, which was related to decreased inflow of warm Atlantic water and increased inflow of cold, deep Norwegian water (Reid et al., 2003). During this period, dinoflagellates, diatoms, decapod larvae, copepods, herring and western mackerel stocks were in low numbers, but Arctic-boreal plankton species and *A. aurita* and *C. lamarckii* medusae were particularly abundant. The authors speculate that the south-eastern North Sea (e.g. WND) is more affected by atmospheric–sea interactions, while the northern region (e.g. NOS) is more affected by oceanic conditions and advection. In summary, the negative phase of the NAO produced conditions that were favourable to high jellyfish abundances in most of the North Sea, but positive NAOI were most favourable at the northernmost site, where correlations between the NAOI and SST switch from positive to negative. Cold conditions were associated with high medusa abundance in all locations.

Chrysaora melanaster *Brandt scyphomedusae in the Bering Sea and Gulf of Alaska*

Bottom trawl surveys by the US National Marine Fisheries Service (NMFS) provided bycatch data for jellyfish biomass (primarily *Chrysaora melanaster*, a large, boreal species) over the eastern Bering Sea shelf during June through August, 1979–1997 (Brodeur et al., 1999). Medusa biomass increased gradually from 1979–1989, but then increased ten-fold between 1982–1989 and 1990–1997 (Figure 6). This dramatic increase occurred simultaneously with a shift from predominantly negative North Pacific Pressure Indices (NPPI) in 1975–1989 to positive NPPI in 1990–1997. Years with positive NPPI correspond with reduced cloud cover, increased solar radiation and increased sea surface water temperatures (SST).

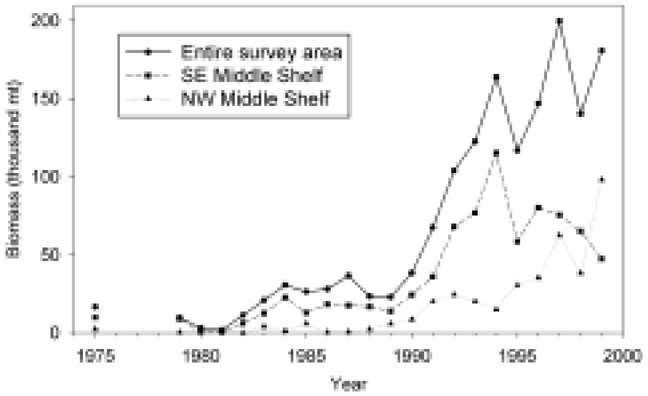

Figure 6. Biomass of medusae, primarily *Chrysaora melanaster*, caught in trawls in the south-eastern Bering Sea 1979–1997 (from Brodeur et al., 2002).

Small-mesh trawl surveys, conducted by the NMFS and the Alaska Department of Fish and Game in May–October, 1953–1997, provided by-catch data for jellyfish in the coastal Gulf of Alaska (GOA) (Anderson & Piatt, 1999). They compared catch data for 35 taxa (including jellyfish) with four climate indices, NPPI, coastal SST, GOA air temperature, and GOA water temperature at 250 m. All four indices were negative in the 1970s and generally negative before 1970; however, the indices abruptly switched in about 1977 to strongly positive during the 1980s, and remained mostly positive in the 1990s. Thus, a cold regime shifted to a warm regime in 1977. When the climate indices were negative, the catch was predominated by shrimp. After the shift to positive indices, the catch changed to predominantly gadids and flatfish. An increase in the jellyfish catch began about 1977, with a dramatic increase in the late 1980s, as seen in the Bering Sea.

Thus, dramatic increases in jellyfish biomass in Alaskan waters in the 1980s and 1990s followed a climate shift from a cold to a warm regime. The causes for the jellyfish increases are not known, in part, because nothing is known about the ecology of the polyps. Brodeur et al. (1999) speculated that food web effects may be responsible. After the regime shift in 1989, greater ice cover in the south-eastern Bering Sea could have led to a more stable, warmer, and more productive surface layer after the ice melted (Hunt et al., 2002). Alternatively, biomasses of medusae were inversely correlated with forage fish, which are potential competitors with medusae for zooplankton foods; thus heavy fishing may have released medusae from competition with forage fish (Brodeur et al., 2002). In spite of continued warming since 2000, jellyfish populations have decreased substantially in the Bering Sea, which may be due to climatically-induced changes in the ecosystem (R.D. Brodeur, personal communication).

Mastigias *sp. scyphomedusae from Jellyfish Lake, Palau, Micronesia*

Golden jellyfish, *Mastigias* sp., occur perennially in high numbers in several tropical marine lakes in Palau. Medusae in Jellyfish Lake were estimated to number 1.8 million in 1996 (Dawson et al., 2001). The strong 1997–1998 El Niño Southern Oscillation (ENSO) event may have caused the disappearance of *Mastigias* sp.

from the lake. A dramatic decline was noticed in the autumn of, 1998, and medusae had virtually disappeared by March 1999 (Dawson, 2005). Mortality of large medusae occurred first, before November 1998, mortality of recently-strobilated medusae occurred between late-1998 and April 1999, and strobilation ceased by May 1999. The cause of these changes appeared to be an unusually warm, salty, and strongly-stratified water column, which probably was initiated by the 1997–1998 ENSO. Field-collected polyps were not strobilating and had no zooxanthellae (Table 1), which are required for strobilation. Laboratory experiments showed that mortality of medusae increased dramatically above 34°C, and that zooxanthella densities in the polyps decreased at both low (<25) and high (>40) salinities, and at high temperatures (>33°C). Thus, unusually warm temperatures and high salinities apparently caused the mortality of medusae and loss of zooxanthellae (bleaching) from the polyps, preventing strobilation. By contrast, conditions in Goby Lake were not as extreme, and did not cause medusae to disappear (Table 1). Thus, tropical *Mastigias* sp. living in very warm water, could not tolerate conditions associated with the strong ENSO event. Medusae of *Aurelia* sp., which does not have zooxanthellae, were present in Jellyfish Lake throughout the ENSO event (Dawson et al., 2001).

Holoplanktonic hydromedusae and siphonophores in the Mediterranean Sea

The holoplanktonic hydromedusa, *Liriope tetraphylla* (Chamisso & Eysenhardt), is widely distributed from about 40°N to 40°S. From weekly 10 m^3 samples in Villefranche Bay, Buecher et al. (1997) evaluated interannual differences in abundance of *L. tetraphylla* (<3 cm bell diameter), and compared those with periods of *Pelagia noctiluca* scyphomedusa occurrence and with temperature and salinity patterns in 1966–1993. The greatest hydromedusan abundance was after 1984 during a warm (>17.5°C), saline (salinities >38.0) period, however, Buecher et al. (1997) did not report a significant relationship between their abundance and climatic factors. Periods of very low hydromedusan abundance corresponded with *P. noctiluca* occurrence in 1969–1970 and 1981–1984. Low abundances of the hydromedusae may have been due to predation on them by the scyphomedusae, which are known to eat hydromedusae and other gelatinous taxa (reviewed in Purcell et al., 1999b), and the effects of climate possibly were obscured.

Buecher (1999) used the same samples to determine long-term trends of the small calycophoran siphonophores *Chelophyes appendiculata* (Eschscholtz) and *Abylopsis tetragona* (Otto), as well as additional depth-specific samples in 1994–1995 to determine vertical distribution relative to temperature and salinity. The two siphonophore species showed different temperature and depth preferences, with *C. appendiculata* occurring mostly in the summer in the surface layer at warm temperatures (19–25°C) and *A. tetragona* occurring in cool water (<19°C) during the spring and below the warm surface layer. Both species, however, were most abundant after 1980, when a hypersaline (salinities >38.0) period began, and were especially abundant after 1984, when a warm (>17.5°C) period coincided with high salinities. In addition to experiencing favourable climate conditions, the siphonophores and the hydromedusae could have been released from predation by the scyphomedusan *P. noctiluca* after 1984.

Table 1. *Temperature, zooxanthellae content and reproductive condition of* Mastigias *sp. polyps in two marine lakes in Palau, Micronesia in 1999 (modified from Dawson et al., 2001).*

	Jellyfish Lake	Goby Lake
Water temperature 1978–1998 (°C)	30.9	30.4
Dates in 1999	26 Jul–4 Sep	12 Jan
Water temperature 1999 (°C)	32.4–33.2	31.4
Number of polyps collected	1215	305
Polyps with zooxanthellae (%)	~2	89
Zooxanthellae density index (0–3)	0.02	1.10
Strobilating polyps (%)	0	9

Holoplanktonic Aglantha digitale *(O.F. Müller) hydromedusae off Greenland*

Aglantha digitale hydromedusae (<4 cm bell height) are abundant in temperate to boreal waters above 200 m depth in the Atlantic and Pacific (Wrobel & Mills, 1998). The abundance of total zooplankton and numerous individual taxa, including *A. digitale*, were compared with trends in temperature and salinity from June to July during 1950–1968 (Pedersen & Smidt, 2000). *Aglantha digitale* numbers were significantly and positively correlated with temperature ($P<0.005$), and less strongly with salinity ($P=0.03$). Water temperatures were unusually warm until 1961 (peak 4.5°C), and then decreased to unusually cold temperatures of about 1°C in 1969–1971, which was attributed to increased flow of the East Greenland Polar Current, after which temperature rose again. Hydromedusan abundances closely followed that pat-

Table 2. *Mean (± SD) surface water temperatures and salinities during herring egg incubation (from Purcell et al., 1990) and mean densities of* Aequorea victoria *hydromedusae when the herring larvae hatched after incubation (from Purcell & Arai, 2001) in Kulleet Bay, British Columbia, Canada.*

Dates of incubation	Temperature (°C)	Salinity	Medusae (no. m^{-3})
08–22 Mar 1983	9.3 ±0.4	27.2 ±0.6	0.012
22 Mar–05 Apr 1984	9.4 ±0.5	27.8 ±0.3	0.35
01–14 Apr 1985	9.2 ±0.2	29.1 ±1.1	1.1
16–30 Mar 1986	8.2 ±0.2	29.0 ±0.5	<0.006
12–23 Mar 1987	8.4 ±0.4	28.8 ±0.4	0.02

tern. Two forms of *A. digitale* were distinguished; the predominant white form was positively correlated with temperature ($P<0.005$), and a red form showed a negative correlation ($P<0.005$). The red form also was positively correlated with salinity ($P=0.02$), and was associated with increased flow of cold, Arctic water. Zooplankton abundances also were positively correlated with temperature, suggesting increased productivity in the region during warm conditions.

Aequorea victoria *(Murbach & Shearer) hydromedusae in the northeastern Pacific*

Aequorea spp. are very large hydromedusae (<25 cm bell diameter) with species found around the world (Bouillon, 1999; Purcell, 2003; Sparks et al., 2005). *Aequorea victoria* has comparatively small (<7 cm) medusae that are abundant in the Puget Sound region and are important predators of fish eggs and larvae (Purcell, 1989; Purcell & Grover, 1990). Medusae were sampled in a bay of Vancouver Island for five springs when the herring larvae hatched (Table 2). Mean densities of *A. victoria* medusae were positively and significantly related to mean temperatures ($P=0.01$) and salinities ($P<0.01$) (multiple linear regression, $r^2=0.984$, $F=60.6$, $P=0.016$), with the greatest densities in 1985 at high temperature and salinity.

Mesopelagic hydromedusae in Monterey Bay, north-eastern Pacific

Records of hydromedusae, temperature and salinity were made from 1990–1998 using a remotely operated vehicle (ROV) between 100 and 900 m depth in Monterey Bay (Raskoff, 2001). Positive anomalies of 'spiciness', which combines temperature and salinity, corresponded with intrusions of warm, salty water during the strong 1991–1992 and 1997–1998 ENSO events. *Mitrocoma cellularia* (A. Agassiz) is a common temperate to boreal species in the north-eastern Pacific, with hydromedusae (<9 cm bell diameter) found at epipelagic to mesopelagic depths (Wrobel & Mills, 1998). Periods of *M. cellularia* abundance closely matched the positive spiciness signals, with peak abundance following the onset of warm, high salinity conditions by several months (Figure 7). The medusae were found at temperatures of 4.2–14.1°C and salinities of 32.4–34.7. This species buds medusae from benthic polyps; it was unknown if the medusae were transported into the bay in the warm, salty water, or if local populations responded to the intrusion. By contrast, *Colobonema sericeum* Vanhöffen was in more restricted temperature, salinity and dissolved oxygen conditions, and occurred in greater numbers between, rather than during, ENSO events. The holoplanktonic hydromedusan, *C. sericeum* (<4.5 cm diameter), is found in the upper mesopelagic Pacific, Atlantic and Indian oceans (Wrobel & Mills, 1998). Thus, mesopelagic populations of two hydromedusan species were affected differently by warm, salty conditions associated with ENSO events. As illustrated in the above correlations between jellyfish and environmental factors, the complexity of ecosystems and the multiplicity of changes frustrate deduction of cause and effect, which experimental studies may help to elucidate.

Environmental effects on asexual reproduction of benthic polyps of jellyfish

Aurelia *spp. scyphomedusae*

Most studies of strobilation have been on *Aurelia aurita* (e.g. Thiel, 1962; reviewed in Spangenberg, 1968; Arai, 1997; and Lucas, 2001). Strobilation requires iodine and is accompanied by production of thyroxin (Spangenberg, 1967, 1971). Many studies focus on factors that trigger strobilation, such as decreasing temperature and food (e.g. Ishii & Watanabe, 2003). Increased food and temperature increase the rate of strobilation, or number of disks or ephyrae produced (reviewed in Spangenberg, 1968; Arai, 1997; and Lucas, 2001). Custance (1964) reported that light inhibited strobilation. Because of the extreme differences among their habitats, responses of different populations of *Aurelia* spp. to environmental cues would differ (Albert, 2005). For example, in temperate waters of the northern Atlantic, strobilation is in autumn or winter, ephyrae are present in spring, and medusae with planulae occur in summer; by contrast, in tropical waters, ephyrae and medusae may be present all year (reviewed by Lucas, 2001).

The combined effects of temperature and salinity were tested on *Aurelia labiata* Chamisso & Eysenhardt (Purcell, unpublished data). Polyps from their native temperate eastern Pacific waters (Gershwin, 2001)

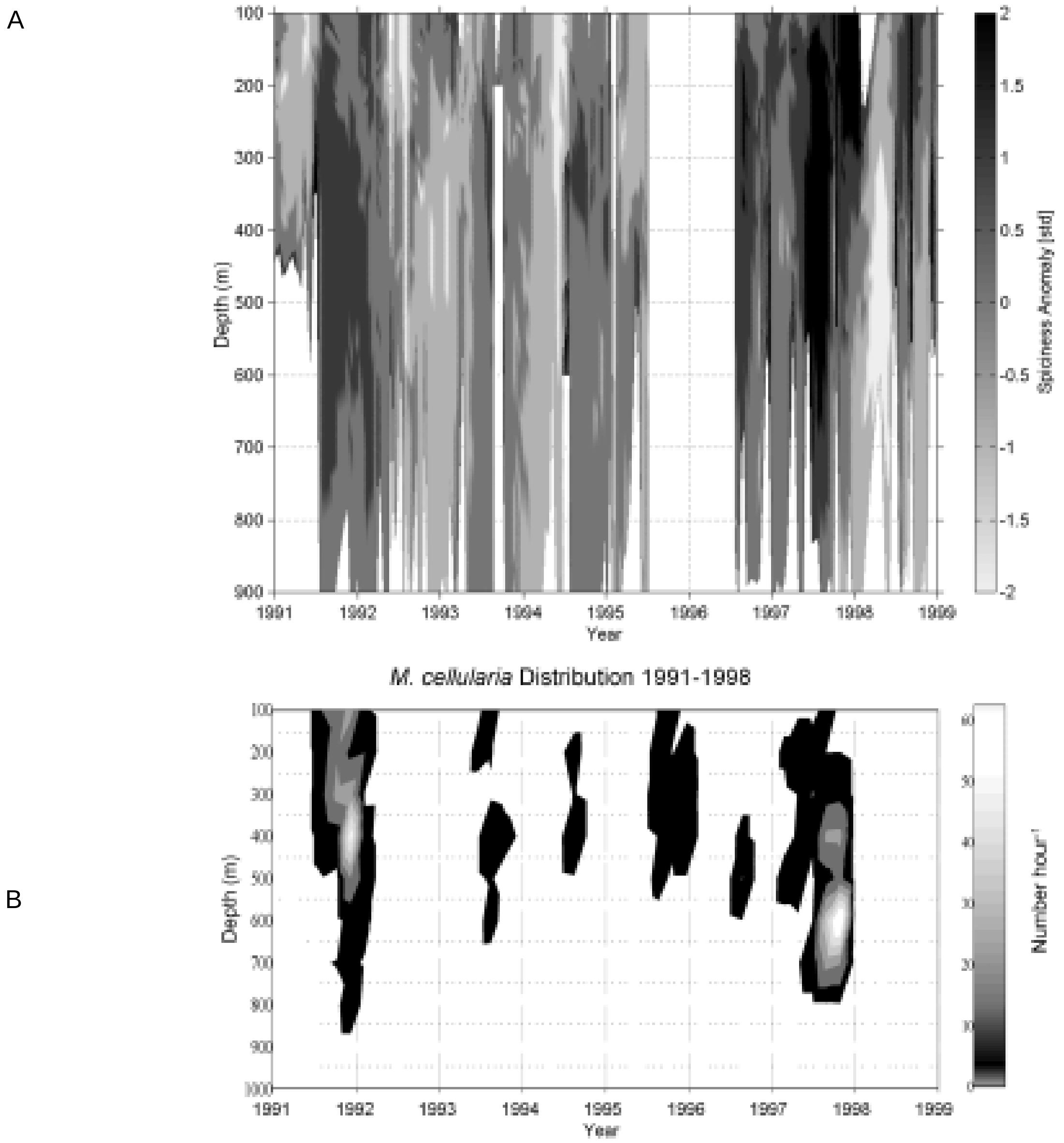

Figure 7. Contours of (A) spiciness anomalies, and (B) vertical distribution and abundance of *Mitrocoma cellularia* hydromedusae in Monterey Bay, California from 1991–1998 (from Raskoff, 2001).

were collected at 10°C and 27 salinity, and tested in nine combinations of temperature (7, 10, 15°C) and salinity (20, 27, 34), which span local extremes. Dramatically more ephyrae were produced at warmer temperatures (Figure 8). Temperature, salinity and their interaction significantly affected the number of new polyps produced ($P<0.0001$, $P<0.01$ and $P<0.001$, respectively), but only temperature affected the numbers of ephyrae produced ($P<0.0001$) (2-way analysis of variance). Ephyra production began earlier and was completed more quickly at warmer temperatures ($P<0.001$), with two cycles of strobilation at 15°C rather than one, as at the cooler temperatures. No viable ephyrae were produced at 7°C. Thus, the numbers of ephyrae and the proportions of ephyrae relative to polyps budded were greatest, and strobilation was most rapid at the warmest temperature tested. Growth of ephyrae also increased with temperature (Widmer, 2005).

Chrysaora quinquecirrha *scyphomedusae*

Studies on *Chrysaora quinquecirrha* in the 1970s in Chesapeake Bay were designed to determine the conditions that triggered strobilation. Strobilation occurs after prolonged chilling and rewarming when temperatures reach 17°C in the spring (Loeb, 1972). Longer periods of illumination (0, 10, 24 h d^{-1}) accelerated strobilation (Loeb, 1973). Strobilation depends on iodide and the synthesis of thyroxin (Black & Webb, 1973; Silverstone et al., 1978). Iodide is directly pro-

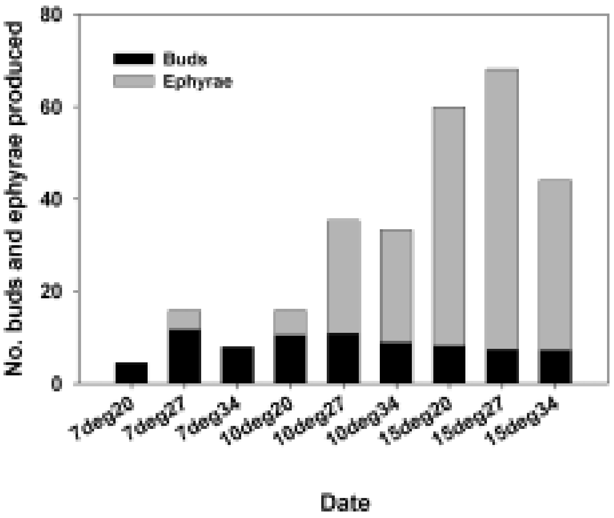

Figure 8. Numbers of buds and ephyrae produced by *Aurelia labiata* polyps from the north-eastern Pacific. Polyps in individual 10 ml wells were maintained for 104 d with bi-weekly feeding and cleaning. Treatments were combinations of temperature (7, 10, 15°C) and salinity (20, 27, 34). Numbers are means of 24 polyps in each treatment (Purcell, unpublished data).

portional to salinity, and ranges from about 70–470 nM at salinities of 5–35 (Luther & Cole, 1988). At very low salinities, iodide may be insufficient for strobilation.

Experiments were conducted on polyps of *C. quinquecirrha* in order to explain the distribution of medusae in Chesapeake Bay (salinities of 5 to 25) and their dramatic interannual variations in abundance (Cargo & Schultz, 1967; Cargo & King, 1990; Purcell et al., 1999c). Combinations of temperature (15, 20, 25°C) and salinity (5, 10, 15, 20, 25, 30, 35) showed that ephyra and polyp production were significantly reduced at both low (≤10) salinities ($P<0.001$, $P=0.002$) and high (≥25) salinities ($P=0.013$, $P=0.034$) (Figure 9; Purcell et al., 1999c). Warmer temperatures increased the number of ephyrae, but effects were significant ($P=0.002$) only at high salinities (25, 30). Each 5°C increase shortened the time to strobilate by about one week. Temperature effects on polyp production were not significant. More ephyrae, but not more polyps, were produced with more available prey. The distribution of *C. quinquecirrha* in Chesapeake Bay and these results suggest that this is a mesohaline ecotype. The species also occurs in higher salinity waters from New England through the Gulf of Mexico, where the polyps may have very different responses to salinity and temperature.

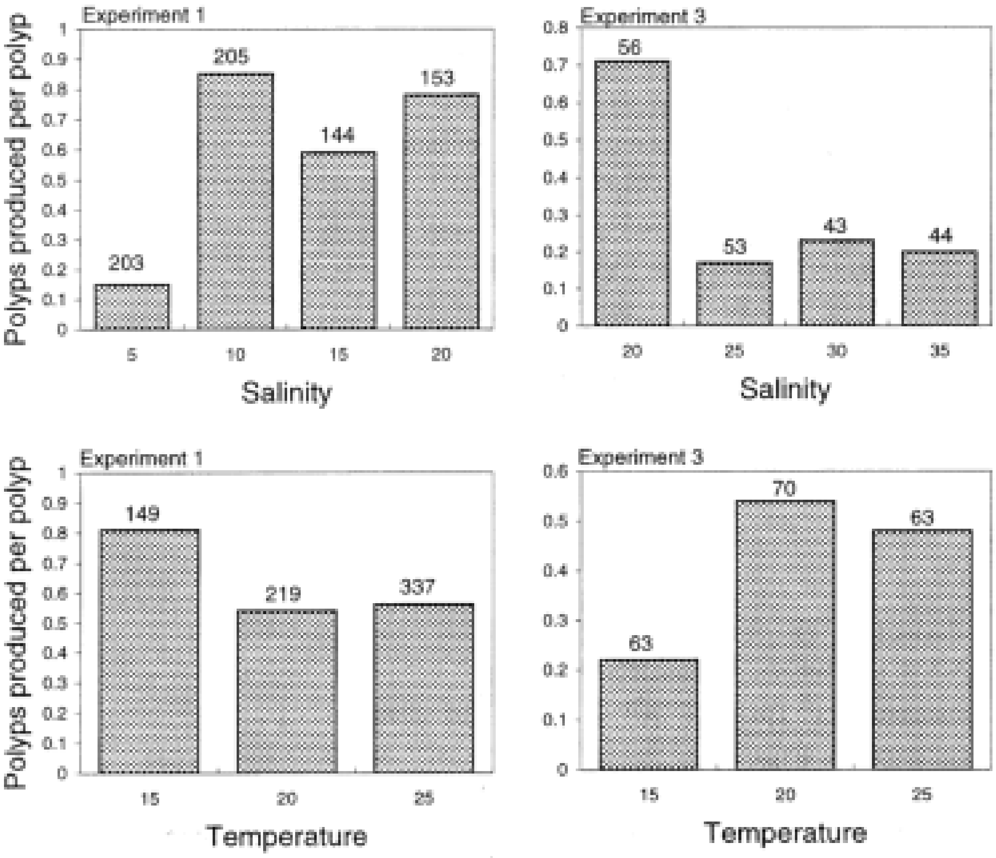

Figure 9. Numbers of ephyrae produced by polyps in combined temperature and salinity treatments. Each salinity bar represents the mean of three temperature treatments. Similarly, each temperature bar represents the mean of four salinity treatments. Initial numbers of polyps are given above each bar. Food levels were lower in Experiment 1 than in Experiment 3, which explains the difference in numbers of ephyrae produced (from Purcell et al., 1999c).

Rhopilema esculenta *Kishinouye scyphomedusae in south-east Asia*

Rhopilema esculenta, the most expensive species in the Asian jellyfish fisheries, is distributed in western Japan, Po Hai, Yellow Sea and the East and South China Seas (Omori & Nakano, 2001). Survival of planulae, polyps, and ephyrae were reduced in low (≤10) salinity treatments (Lu et al., 1989). Strobilation of polyps and growth of ephyrae were greatest at salinities of 10–24, but persisted at the highest salinity tested (31.4). Marked decreases in the catch of jellyfish occurred during three periods between 1973 and 1985, which the authors attribute to unusually high freshwater inputs into the estuaries where the polyps live, thereby reducing survival and strobilation.

Stylactis (Hydractinia) hooperi (*Sigerfoos) hydromedusae*

Stylactis (Hydractinia) hooperi hydroids are associated with gastropods and their shells inhabited by hermit crabs in Brazil. Hydroid colonies collected from 20–29.5°C and 33–35 salinity were transferred to combinations of temperature (10, 15, 20, 25, 30, 35) and salinity (15, 25, 35, 45, 55) (Nipper-Buscariolli & Moreira, 1983). Colonies showed 100% mortality at extreme temperatures (10 and 35°C) and salinities (15 and 55). Over three weeks, the best growth of colonies was at 20°C and 25–35 salinity. Medusa buds developed only in a few treatments, specifically, 20–30°C in combination with 35–45 salinity. The best budding of females occurred at 30°C and 25 salinity.

Moerisia lyonsi *(Boulenger) hydromedusae*

Moerisia lyonsi is a small species (<2 cm bell diameter) that was introduced to Chesapeake Bay sometime prior to 1966 when it was first recorded (Calder & Burrell, 1967). It is thought to have originated in oligohaline waters of eastern Europe (Dumont, 1984); however, it thrived (≤13.6 medusae l^{-1}) in mesohaline (9–12 salinity) mesocosms, suggesting broader salinity tolerances (Purcell et al., 1999a). Two kinds of buds are produced by *M. lyonsi*, one becomes polyps and the other becomes medusae. Rates of asexual reproduction increased dramatically from 0.25 to 3.86 buds polyp^{-1} d^{-1} with food levels of 1 to 8 copepods polyp^{-1} d^{-1}. In 45 combinations of temperature and salinity, *M. lyonsi* polyps survived direct transfer from 12 to 1–40 salinity and from 22°C to 10–29°C temperatures (Ma & Purcell, 2005a). Mortality within 7 d was observed only at high salinity (35, 40) in combination with low temperature (10°C).

Effects of combinations of temperature (20, 29°C), salinity (5, 15, 25), and prey density (4, 8, 12, 16 copepods polyp^{-1} d^{-1}) were tested on asexual reproduction of *M. lyonsi* over 31 d (Ma & Purcell, 2005b). Significant effects were seen from all variables, with the greatest total budding (5.9 ±0.3 buds polyp^{-1} d^{-1}), highest ratio of medusae to total buds (R_m=0.78), and shortest development times (2 d for polyp buds, 8–10 d for medusa buds) at the warmer temperature, the lowest salinity, and most prey. Conversely, at the cooler temperature, highest salinity, and least prey, budding was low, with no medusae produced. The differences in the numbers of buds produced were due to the effects of temperature and salinity on prey consumption; Figure 10 shows that food consumption was reduced at cool temperature (20°C) and at high salinity (25), and that R_m increased with prey consumption. Development of medusae was accelerated by at least two weeks at 29°C over 20°C. *Moerisia lyonsi* showed great environmental flexibility, which is further enhanced by its ability to form resistant cysts at low temperature.

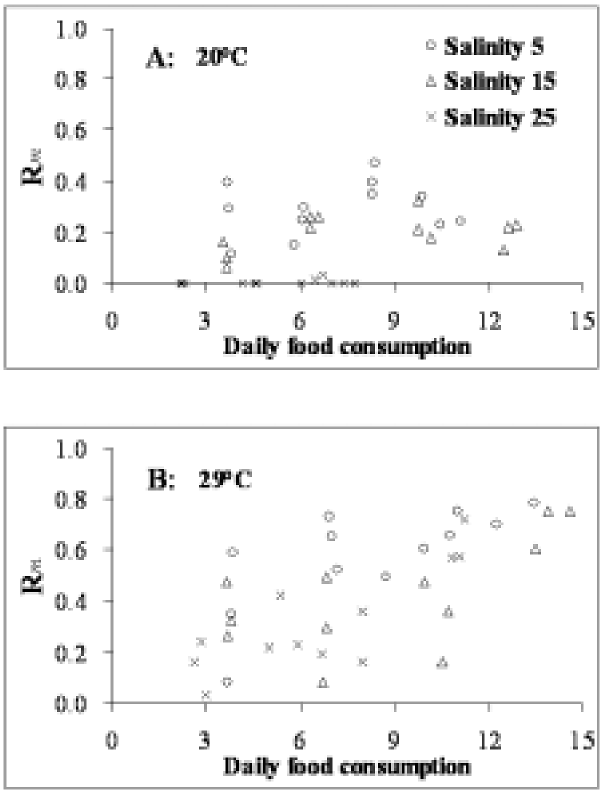

Figure 10. Ratios of the total medusa bud production to total asexual reproduction (R_m) of polyps of the hydromedusan, *Moerisia lyonsi*, in a 31 d experiment in relation to temperature, salinity and daily food consumption. Each polyp was provided with 4, 8, 12, or 16 copepods d^{-1}. (A) at 20°C; (B) at 29°C (from Ma & Purcell, 2005b).

DISCUSSION

Most jellyfish and ctenophore species for which there are data on abundance and climatic conditions are from temperate regions, where populations and conditions undergo large seasonal fluctuations. Some temperate species studied appear to be limited by cold temperatures. *Mnemiopsis leidyi* ctenophores cannot overwinter in the Sea of Azov because of cold (<4°C) winter temperatures, and ctenophores were larger in warmer spring temperatures (Purcell et al., 2001). *Pelagia noctiluca* scyphomedusae cannot overwinter in the northern Adriatic because of low (<10°C) temperatures (Purcell et al., 1999a). *Moerisia lyonsi* did not produce medusa buds at 10°C (Ma & Purcell, 2005b), and apparently overwinters as cysts (Purcell et al., 1999a).

For most temperate species, warm temperatures lead to large numbers of jellyfish and ctenophores, and increased asexual reproduction in scyphozoans and hydrozoans. Sexual reproduction also increases at warm temperatures. Size-specific egg production of *Mnemiopsis leidyi* was significantly greater at warm temperatures (15, 19, and 25–27°C) than at cool temperature (9°C) (Purcell et al., 2001, and unpublished data). Egg production rates of *Chrysaora quinquecirrha* medusae were greater in warmer temperatures (20, 25, 30°C) than at 15°C (Asplen & Purcell, unpublished data). Warming temperatures may allow temperate species to increase their distributions, to overwinter in active condition, to have longer and more prolific reproductive seasons, and to achieve larger populations.

The opposite result of warming may occur for tropical species. Species living at warm temperatures may be unable to tolerate further warming, and their distributions may shift towards cooler water, and they may have shorter active seasons. The upper temperature limit may be 34–35°C for many species (Gatz et al., 1973; Nipper-Buscariolli & Moreira, 1983; Dawson et al., 2001). Scyphozoans are known to form cysts in response to adverse conditions, including both low and high temperatures (reviewed in Arai, 1997), which may enable them to endure stressful conditions.

Generalizing broadly from results of these few studies could lead to erroneous conclusions. Different species in the same environment may respond differently to changing conditions, for example, only one of two mesopelagic hydromedusan species increased in warm, salty conditions of an ENSO event in Monterey Bay (Raskoff, 2001). Anderson & Piatt (1999), show equal proportions of 35 taxa increased, decreased, or had variable responses to the climate shift in the Gulf of Alaska in the late 1970s. Responses to environmental conditions even differ among populations of the same species (Pederson & Smidt, 2000; Lucas, 2001).

There are now recognized approximately 190 species of scyphomedusae (Arai, 1997), 840 species of hydromedusae (Boullion & Boero, 2000), 200 species of siphonophores (Pugh, 1999), and 150 species of ctenophores (Mianzan, 1999). Little is known about the population abundance or dynamics of most of those species. Furthermore, the identities or locations of the polyps are unknown for many of the scyphozoan and hydromedusan species. One goal of this review is to stimulate studies that address environmental effects on the population dynamics of these under-studied organisms.

Although the studies reviewed here are for only a few species and locations, similar incidences probably are wide-spread. The genera *Aurelia, Chrysaora, Cyanea* and others have worldwide distributions, with polar to equatorial representatives. Some species (e.g. *Aurelia* sp., *Mnemiopsis leidyi, Moerisia lyonsi*) have expanded their distributions to other continents through accidental introductions (e.g. Shiganova, 1998; Mills, 2001; Dawson, 2003; Graham et al., 2003; Ma & Purcell, 2005a,b).

The laboratory experiments exposed polyps to extreme, abrupt and chronic changes in temperature and salinity, whereas, changes *in situ* generally would be less severe, and therefore easier to tolerate. Changes would occur gradually over tidal cycles, seasons, years and decades. Changes *in situ* also may be periodic (e.g. diel or tidal), or short-term (rain) rather than chronic as in the experiments. Even so, the cnidarians tested survived and reproduced after severe changes imposed on them in the laboratory. Cnidarians are renowned for remarkable flexibility in asexual reproduction (reviewed in Boero, 1984; Shostak, 1993; Fautin, 2002). Thus, jellyfish and ctenophore populations probably will be able to tolerate, adapt to, and exploit the gradual changes of climate oscillations and global warming.

Temperature had the most obvious effects on population size and asexual reproduction of jellyfish and ctenophores. Warm temperature was associated with greater abundances or production of one ctenophore species, five scyphomedusan species, six hydromedusan species, and two siphonophore species. Other species did not fit this trend (three species of scyphomedusae in the North Sea and one in the tropics, and one species of hydromedusae). In temperate species tested, the numbers of medusae produced, the proportions of new medusae relative to new polyps, and the speed of production were greatest at the warmest temperatures tested. Most attention has been paid to temperature effects, in part because of the marked seasonal and interannual differences, and because of the obvious warming trend of the Earth's climate.

Salinity also changes seasonally and interannually, but the differences usually are more subtle than for temperature. The importance of salinity is obvious in estuaries like Chesapeake Bay, where salinity ranges from 0–30, and salinity significantly affected population size and asexual reproduction of cnidarians there. Salinities also had significant effects on species living where salinity was less variable.

Temperature and salinity affect physiological processes directly. Both low and high temperatures can disable enzymes and transport systems, which physiologically restricts organisms to their adapted temperature ranges (Kinne, 1970). Within the appropriate ranges, low temperatures slow and high temperatures accelerate metabolism and reproduction. Direct effects of salinity may occur (Kinne, 1971), as for *Chrysaora quinquecirrha*, which cannot osmoregulate at salinities ≤5 (Wright & Purcell, 1997), and which may have insufficient iodine at low salinities for strobilation. Temperature and salinity both affected prey consumption by hydrozoan polyps (Ma & Purcell, 2005b).

Environmental changes also undoubtedly have indirect effects on jellyfish and ctenophore populations through the food web. Such effects differ among habitats; for example, in Chesapeake Bay, high precipitation and river flow lead to high nutrient loading, strong stratification, and increased production (Harding et al., 1999), while in the south-eastern Bering Sea, ice cover may increase water column stability and increase production (Hunt et al., 2002). Changes that increase zooplankton abundance would benefit jellyfish and ctenophores. All results indicate that more food increases production of medusae (Thiel, 1962; Purcell et al., 1999a,c; Stibor & Tokle, 2003; Ma & Purcell, 2005b). Parsons & Lalli (2002) discuss how pollution, eutrophication, overfishing, and climate changes can lead to a low-energy food chain that favours nanophytoplankton and jellyfish, in contrast to a high-energy food chain based on diatoms that supports vertebrate predators. Such ecosystem disruptions are occurring in marine and estuarine systems worldwide, and jellyfish and ctenophore populations may benefit.

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