

REVIEW

# Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review

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**ABSTRACT:** Although recent articles state that jellyfish populations are increasing, most available evidence shows that jellyfish abundances fluctuate with climatic cycles. Reports of increasing problems with jellyfish, especially in East Asia, are too recent to exclude decadal climate cycles. Jellyfish are infamous for their direct negative effects on human enterprise; specifically, they interfere with tourism by stinging swimmers, fishing by clogging nets, aquaculture by killing fish in net-pens and power plants by clogging cooling-water intake screens. They also have indirect effects on fisheries by feeding on zooplankton and ichthyoplankton, and, therefore, are predators and potential competitors of fish. Ironically, many human activities may contribute to increases in jellyfish populations in coastal waters. Increased jellyfish and ctenophore populations often are associated with warming caused by climate changes and possibly power plant thermal effluents. Jellyfish may benefit from eutrophication, which can increase small-zooplankton abundance, turbidity and hypoxia, all conditions that may favor jellyfish over fish. Fishing activities can remove predators of jellyfish and zooplanktivorous fish competitors as well as cause large-scale ecosystem changes that improve conditions for jellyfish. Aquaculture releases millions of jellyfish into Asian coastal waters yearly to enhance the jellyfish fishery. Aquaculture and other marine structures provide favorable habitat for the benthic stages of jellyfish. Changes in the hydrological regime due to dams and other construction can change the salinity to favor jellyfish. Accidental introductions of non-native gelatinous species into disturbed ecosystems have led to blooms with serious consequences. In many coastal areas, most of these environmental changes occur simultaneously. We summarize cases of problem jellyfish blooms and the evidence for anthropogenic habitat disruptions that may have caused them. Rapid development in East Asia makes that region especially vulnerable to escalating problems. We conclude that human effects on coastal environments are certain to increase, and jellyfish blooms may increase as a consequence.

**KEY WORDS:** Eutrophication · Fish · Aquaculture · Climate · Warming · Temperature · Zooplankton · Salinity · Sting · Powerplant · Introduce

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## INTRODUCTION

Recent concerns that jellyfish populations are increasing have stimulated speculation about possible causes including climate change, eutrophication, over fishing and invasions (e.g. Arai 2001, Mills 2001, Oguz 2005a,b, Purcell 2005, Hay 2006, Graham & Bayha 2007). While speculation is abundant, evidence for sustained increases is lacking. Analyses of several long-

term (8 to 100 yr) trends in jellyfish populations demonstrate that their abundances vary with climate, often at decadal scales (reviewed in Purcell 2005). Some evidence suggests continued upward trends (Attrill et al. 2007); however, recent time series are still too short to exclude circa-decadal climate cycles. Even though blooms of newly introduced species also vary over time, the invaders may spread into new areas (reviewed in Graham & Bayha 2007). Reports of human

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problems with jellyfish have increased and have captured public attention (e.g. Whiteman 2002, Carpenter 2004, de Pastino 2006, 2007, Owen 2006). Such problems come mainly from jellyfish stinging swimmers and interfering with fishing, aquaculture and power plant operations.

Generally, only a relatively few coastal species of large scyphomedusan jellyfish are responsible for the reported problems. These large species are conspicuous; however, they are only a portion of the diverse gelatinous fauna. Approximately 190 species of scyphomedusae (Arai 1997), 20 species of cubomedusae (Mianzan & Cornelius 1999), 840 species of hydromedusae (Boullion & Boero 2000), 200 species of siphonophores (Pugh 1999) and 150 species of ctenophores (Mianzan 1999) are now recognized. Therefore, the potential for further problems with jellyfish may be very great. In the present review, we discuss only the zooplanktivorous gelatinous taxa mentioned above. We refer to scypho-, cubo-, and hydromedusae as 'jellyfish' for the sake of simplicity.

The ability of gelatinous species to occur in large numbers (i.e. to bloom) is due to the cnidarians (Scyphozoa, Cubozoa, Hydrozoa) having both asexual and sexual reproduction. Most coastal jellyfish are asexually budded from an attached stage in the life cycle, a scyphistoma for scyphozoans, and a hydroid (often colonial) for hydromedusae. We will refer to the benthic stages as 'polyps'. Polyps bud more polyps, and many jellyfish can be budded from a single polyp; cubozoan polyps are an exception, transforming into individual jellyfish without budding. Swimming jellyfish reproduce sexually, often have great fecundity and may brood the larvae, which settle to become polyps. Temperate species typically have an annual cycle, with small jellyfish (1 to 2 mm ephyrae for scyphozoans) being produced in fall or spring, and the jellyfish growing to sexual maturity over the summer; in the tropics, jellyfish production can occur all year (reviewed in Lucas 2001). By contrast, siphonophores (also cnidarians) and ctenophores lack an attached stage in the life cycle (i.e. holoplanktonic). The siphonophores also have asexual multiplication of reproductive individuals, followed by sexual reproduction. Most ctenophores are hermaphroditic, and have direct development and great fecundity. Therefore, siphonophores and ctenophores are not constrained to one generation per year, in contrast to many species in the other taxa. Although this represents a general picture of the life cycles, cnidarians, especially the hydrozoans, are renowned for reproductive variety (Boero et al. 2002). Many hydromedusae are holoplanktonic (holoplanktonic species indicated by an asterisk in our tables), while this is rare in scyphozoans, and some hydromedusan

jellyfish reproduce asexually (Boero et al. 2002). Thus, the ability of pelagic cnidarians and ctenophores to bloom in good conditions is intrinsic.

Gelatinous predators have important ecological effects that are considered to be detrimental to human interests. They eat zooplankton and can reduce and change zooplankton populations; therefore, they can reduce the food available to fish. They eat ichthyoplankton (eggs and larvae of fish) as well as juvenile fish, and, thus, directly reduce fish populations. These potential effects of jellyfish on fish have been reviewed previously (Purcell 1985, Arai 1988, Bailey & Houde 1989, Purcell & Arai 2001) and will not be considered in detail in this review. Studies showing negative effects of jellyfish on fish recruitment are almost non-existent (but see Lynam et al. 2005).

In this review, we examine recent cases where jellyfish blooms have increased, describe the problems jellyfish directly cause for humans, and show how a number of human activities may increase pelagic cnidarian and ctenophore populations. We focus on species for which factors contributing to the blooms have been analyzed or inferred. Concern about blooms of jellyfish and ctenophores has stimulated several meetings and special volumes that contain more detailed information. The first 2 meetings regarded blooms of *Pelagia noctiluca* scyphomedusae in the Mediterranean Sea (UNEP 1984, 1991). Several meetings focused on the outbreak and spread of *Mnemiopsis leidyi* ctenophores (e.g. GESAMP 1997, Dumont et al. 2004). Meetings and publications that were not targeted on any specific species include Purcell et al. (2001a), CIESM (2001), and JMBA (2005). Various authors have suggested anthropogenic causes for changes in jellyfish populations (e.g. Mills 1995, 2001, Benović et al. 2000, Arai 2001, Graham 2001, Parsons & Lalli 2002, Oguz 2005b). We review these topics on a global scale and present information that is as comprehensive as possible. We present data from East Asia where blooms have increased recently.

## ARE JELLYFISH POPULATIONS INCREASING?

The paucity of long-term data makes it difficult to draw definitive conclusions on the status of jellyfish populations. Most analyzed data sets show variations in jellyfish population size with climatic regime shifts at decadal scales (reviewed in Purcell 2005). Even the dramatic increase of *Chrysaora melanaster* during the 1990s in the Bering Sea ended abruptly in 2000, possibly because of exceptionally warm conditions after 2000 (Brodeur et al. in press). Persistent increases of jellyfish unrelated to climate variation have not yet been demonstrated.

Perhaps the best indications that jellyfish blooms have increased are from the reports of problems caused by jellyfish. In the Seto Inland Sea, Japan, *Aurelia aurita* (sensu lato, s. l.) populations have apparently increased since the 1980s, and most dramatically in the last 10 yr; 65% of fishermen surveyed believed that jellyfish had increased during the last 20 yr, while 35% thought they had not (Uye & Ueta 2004). Blooms of the giant Nomura's jellyfish *Nemopilema nomurai* (up to 2 m diameter and 200 kg biomass) have created serious problems in Japanese waters. Before 2000, blooms of *N. nomurai* had been reported only in 1920, 1958 and 1995 in Asian waters; however, beginning in 2002, blooms have occurred every year, except for 2004 (Uye in press). Problems reported with jellyfish (stinging people and interfering with fishing and power plants) in Japan certainly have increased in recent years (Fig. 1, Tables 1 to 4).

Reports of blooms and resulting problems have increased elsewhere in the world as well (Tables 1 to 4). Since the mid-1990s jellyfish have become a problem for fisheries in the East China and Yellow seas, and are associated with decreased fish catches (Cheng et al. 2005). Yan et al. (2004) showed inverse correlations between fish and jellyfish, with greater biomass of *Cyanea* spp. and *Stomolophus* spp. in 1998 to 2003 than in 1990 to 1997. In the northern Benguela Current off Namibia, catches of anchovy and sardines have been reduced dramatically after 1988 compared with those during 1975 to 1988, and large populations of 2 jellyfishes, *Chrysaora hysoscella* and *Aequorea forskalea*, now predominate (Lynam et al. 2006). In addition to interfering in fisheries there, jellyfish have blocked water intakes of power

plants and diamond mining operations (Lynam et al. 2006). Jellyfish populations have bloomed in coastal lagoons along the Mediterranean coasts of Spain and France since the 1990s (Pagés 2001, Anonymous 2006). *Pelagia noctiluca* periodically blooms in the Mediterranean Sea (UNEP 1981, 1984, Goy et al. 1989) and caused problems there in the 1990s (Molinero et al. 2005). In coastal waters of the Middle East, blooms of the rhizostome scyphozoan *Crambionella orsini* have been associated with power- and desalination-plant interruptions since 2000 (Daryanabard & Dawson in press).

It is too soon to know whether these recent jellyfish increases will be sustained or the populations will fluctuate with climate as seen for other species. If environmental deterioration, including ocean warming, is responsible for the blooms, high jellyfish populations may persist.

#### HUMAN PROBLEMS RESULTING FROM JELLYFISH BLOOMS

Stings from pelagic cnidarians cause discomfort and sometimes medical emergencies for swimmers and waders primarily in warm marine waters worldwide (reviewed in Fenner & Williamson 1996, Burnett 2001). Severe stings result especially from cubomedusae and from *Physalia* spp. When pelagic cnidarians occur in great abundance, stinging can occur at epidemic levels (Table 1). In many coastal tourist areas, monitoring and warning systems are used to alert swimmers to potential encounters with jellyfish (e.g. Bernard et al. 1988, Decker et al. 2007). As human populations and recreational activities continue to increase along the coasts, stinging is projected to become an increasing problem (Macrokanis et al. 2004). Beaches infested with jellyfish undoubtedly are detrimental to tourist appeal. Jellyfish also present stinging hazards to fishermen as they pull fishing gear on board and to aquaculturists (Sharp 2001).

Interference with fishing operations is the most frequently reported problem occurring with great abundances of jellyfish (Table 2). Large catches of jellyfish can split the fishing nets and ruin the quality of the catch (Fig. 2). Such problems have been particularly acute for Japan since 1990 when *Aurelia aurita* increased in the Seto Inland Sea, and since 2002 in coastal waters where Nomura's jellyfish has bloomed annually and severely interfered with set-net fisheries. Such problems apparently are more widespread than reported in the literature, as suggested by the many jellyfish-exclusion devices used with fishing gear (e.g. Mohr & Rauck 1978, Broadhurst & Kennelly 1996, Anonymous 1997b, Wienbeck 1998, Van Marlen et al. 2001, Matsushita & Honda 2006).

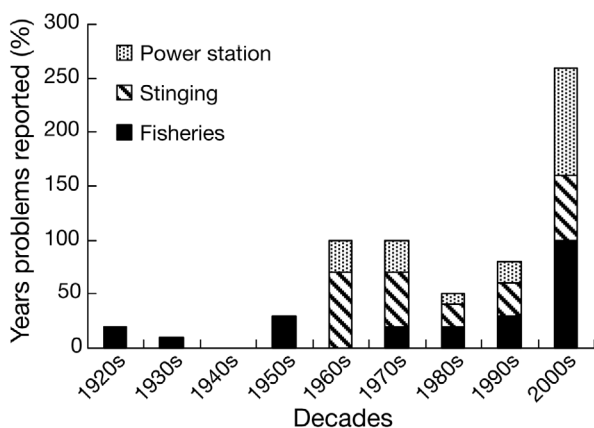


Fig. 1. Percentages of years in each decade having reports of human problems with jellyfish in Japan. Data are from Tables 1 to 4; fisheries and aquaculture problems are combined. Problems can occur every year in each of the 3 categories (stinging, power station, fisheries); therefore, a perfect score is 300%. Reports from the current decade included 2000 to 2005; thus, percentages were calculated for 6 yr rather than 10 yr decade<sup>-1</sup>

Table 1. Published reports of severe stinging events by jellyfish around the world. Species indicated with asterisk (\*) are holo-planktonic; all others have a benthic stage. Pref. = Prefecture

Species	Year (months)	Location	Stinging effects	Source
<b>Asia</b>				
<i>Gonionemus oshoro</i>	1961–63 (Jul–Aug)	Hokkaido, Japan	175 swimmers (88 severe)	Yasuda (1988)
<i>Physalia physalis</i> *	1961 (June)	Kanagawa Pref., Japan	15000 swimmers	Yasuda (1988)
<i>Chrysaora melanaster</i>	1961–63 (Jul–Aug)	Hokkaido, Japan	175 swimmers (88 severe)	Yasuda (1988)
<i>C. melanaster</i>	1976 (Jul–Aug)	Kyoto Pref., Japan	300 swimmers (20 severe)	Yasuda (1988)
<i>C. melanaster</i>	1979 (Jul–Aug)	Fukui Pref., Japan	Several tens of swimmers and fishermen (5 severe, 1 dead)	Yasuda (1988)
<i>C. melanaster</i>	1999 (Apr–Aug)	Sea of Japan coast	Several hundred swimmers and fishermen	Yasuda (2003)
<i>Carybdea rastoni</i> , <i>Gonionemus vertens</i>	1978 (Jul)	Hyogo Pref., Japan	Several tens of swimmers	Yasuda (1988)
<i>Olindias formosa</i>	1979 (Jul)	Nagasaki Pref., Japan	Several tens of swimmers (3 severe, 1 dead)	Yasuda (1988)
<i>Chiropsalmus quadrigatus</i>	1981 (Jul–Sep)	Okinawa Pref., Japan	1 severe	Yamaguchi (1982)
<i>Agalma okeni</i> *	1995 (Jul–Aug)	Fukui Pref., Japan	Several tens of swimmers (3 severe)	Yasuda (2003)
<i>Euphysora bigelowi</i>	2000 (Jul–Aug)	Fukui Pref., Japan	Several tens of swimmers	Yasuda (2003)
<i>Nemopilema nomurai</i>	1991–96	Qingdao, China	8 deaths	Fenner & Williamson (1996)
<i>N. nomurai</i>	2002 and after	Sea of Japan coast	Several hundred fishermen	Kawahara et al. (2007), S. Uye (pers. obs.) Oiso et al. (2005)
<i>Porpita porpita</i> *	2002 and after	Northern Sea of Japan	Swimmers	Oiso et al. (2005)
<b>Australia/Indo-Pacific</b>				
<i>Chironex fleckeri</i>	Annual	Australia, Malaysia, Philippines	67 deaths 2–3 deaths yr <sup>-1</sup> ; 20–40 deaths yr <sup>-1</sup> (1884–1996)	Fenner & Williamson (1996), Bailey et al. (2003)
<i>Carukia barnesi</i> and other species	2002, peak (Jan–Apr)	Tropical Australia; NW Australia	Irukandji syndrome Increasing, 88 in 2001–03	Bailey et al. (2003), Macrokanis et al. (2004)
<i>Physalia</i> sp.*	Annual, 2005–07	Tropical waters	10 000 annually, 30 000 in 2006, 1200 in 1 weekend in 2007	Fenner & Williamson (1996), de Pastino (2007)
<b>Europe</b>				
<i>Pelagia noctiluca</i> *	1984–87, 2004, summer	French Riviera, Monaco	2500 treated, 45 000 treated	Bernard et al. (1988)
<i>P. noctiluca</i> *	2006, (Aug)	Spain, east & south coasts	>14 000 treated	Pingree & Abend (2006)
<i>Cotylorhiza tuberculata</i> , <i>Rhizostoma pulmo</i>	Annual, after 1993	Coastal lagoon, Spain	Concern	Pagés (2001)
<i>Rhopilema nomadica</i>	After 1980	Eastern Mediterranean		Lotan et al. (1993), Gusmani et al. (1997)
<b>North America</b>				
<i>Chrysaora quinquecirrha</i> Chirodroids	Annual, Before 1996	Chesapeake Bay Gulf coast of Texas, USA; Puerto Rico	Considered painful 1 death, serious stings	Burnett (2001) Fenner & Williamson (1996)
<i>Linuche unguiculata</i>	Annual	Southeast coast USA, Brazil	Seabathers eruption	Segura-Puertas et al. (2001)
<i>Physalia physalis</i> *	Before 1996	Florida & North Carolina, USA	3 deaths	Fenner & Williamson (1996)

Jellyfish kill fish in aquaculture pens, with problems reported especially in Japan and Scotland (Table 3). Small jellyfish and tentacles of large species enter the fish pens and irritate the fish gills resulting in hemor-

rhage and subsequent suffocation (Johnston et al. 2005). Decapod culture also has been reported to be affected adversely by jellyfish blooms in India and the USA (Table 3).

Table 2. Published reports of jellyfish interfering with fisheries operations around the world. Pref. = Prefecture, nd = no data available, s. l. = sensu lato. Locations are in Japan unless otherwise stated

Species	Year (months)	Location	Damage to fisheries	Source
<b>Asia</b>				
<i>Nemopilema nomurai</i>	1920 (Oct–Dec)	Sea of Japan coast, Hokuriku and Tohoku Districts	Caught in set net, beach seine, seine net	Kishinouye (1922), Yasuda (1988)
<i>N. nomurai</i>	1922 (Nov)	Hokuriku District	Set net	Kishinouye (1922)
<i>N. nomurai</i>	1938	Sea of Japan coast	nd	Yasuda (2003)
<i>N. nomurai</i>	1958 (Aug–Dec)	Sea of Japan coast, Tsugaru Strait, Pacific coast of northern Japan	Set, trawl, gill and dip nets	Shimomura (1959), Nishimura (1959, 1961)
<i>N. nomurai</i>	1995 (Sep–Dec)	Sea of Japan coast	Set net	Kuroda et al. (2000)
<i>N. nomurai</i>	2002–06 (Aug–Dec)	Sea of Japan coast, Tsugaru Strait, Pacific coast of northern Japan (worst in Fukui and Shimane Pref.)	Set, trawl, gill and dip nets	Yasuda (2003), Kawahara et al. (2006)
<i>Aurelia aurita</i> (s. l.)	1952 (Jul–Sep)	Kyoto, Fukui Pref.	Set net	Yasuda (1988)
<i>A. aurita</i> (s. l.)	1976–77 (Apr–Jul)	Kyoto Pref.	Trawl net	Yasuda (1988)
<i>A. aurita</i> (s. l.)	1981 (Mar–Aug)	Yatsushiro Bay, Kumamoto Pref.	Set net, gill net	Yasuda (1988)
<i>A. aurita</i> (s. l.)	1997 (Mar–Jun)	Sea of Japan coast	Set, trawl and gill nets	Kuroda et al. (2000)
<i>A. aurita</i> (s. l.)	2000–02 (May–Oct)	Seto Inland Sea	Set, trawl and gill nets	Uye & Ueta (2004)
<i>Chrysaora melanaster</i>	1981 (May–Aug)	Fukui Pref.	Gill net	Yasuda (1988)
<i>C. melanaster</i>	1997 (Mar–Jun)	Sea of Japan coast	Set, trawl and gill nets	Kuroda et al. (2000)
<i>C. melanaster</i>	2000–02 (May–Oct)	Seto Inland Sea	Set, trawl and gill nets	Uye & Ueta (2004)
<i>Aequorea</i> sp., <i>Cyanea</i> sp.	Since mid- to late 1990s	Yellow and East China seas, China	Trawl nets	Ding & Cheng (2005), Cheng et al. (2005), Xian et al. (2005)
<i>Sanderia malayensis</i>	2004	Yangtze River estuary, China	Trawl nets	Xian et al. (2005)
<i>Chiropsalmus quadrigatus</i>	1981 (May–Aug)	Okonawa Pref.	Set net	Yamaguchi (1982)
<i>Aequorea coerulescens</i>	1999 (May–Jun)	Fukui Pref.	Set net	Kuroda et al. (2000)
<i>Bolinopsis mikado</i>	1989 (Jun–Aug)	Hiroshima Pref.	Seine net	S. Uye (pers. comm. from local fishermen)
<i>B. mikado</i>	2000–02 (May–Oct)	Seto Inland Sea	Set, trawl and gill nets	Uye & Ueta (2004)
<b>Australia/Indo-Pacific</b>				
Unidentified	Sporadic	Northern Australia	Fill and split prawn trawls	Rawlinson & Brewer (1995)
<b>Africa</b>				
<i>Chrysaora hysoscella</i> , <i>Aequorea forkalea</i>	Since 1988	Northern Benguela Current off Namibia	Reduced and spoiled catches, damaged gear	Lynam et al. (2006)
<b>Europe/Middle East</b>				
<i>Pelagia noctiluca</i>	Cyclic	Mediterranean Sea	Clog fishing nets	Bernard et al. (1988)
<i>Rhopilema nomadica</i>	After 1980	Eastern Mediterranean Sea	Clog fishing nets	Lotan et al. (1993)
<i>Crambionella orsini</i>	2002	Gulf of Oman, Persian Gulf	Decreased catch, damage to gear	Daryanabard & Dawson (in press)
<i>Aurelia aurita</i> , <i>Rhizostoma pulmo</i> , <i>Mnemiopsis leidyi</i>	2006	Coastal lagoons, France	Fouled fishing gear	Anonymous (2006)
<b>North America</b>				
<i>Phyllorhiza punctata</i>	2000 (May–Sep)	Northern Gulf of Mexico, USA	Fouled shrimp gear, reduced harvest, US\$10 million loss, predation on bivalve larvae	Graham et al. (2003)

Jellyfish also clog seawater intake screens of power and desalination plants causing power reductions and shutdowns (Table 4). This has been a long-standing problem in Japan where large near-shore populations

of *Aurelia aurita* (s. l.) jellyfish occur. Similar problems have been reported from other countries. Jellyfish clogging requires ongoing maintenance; one power plant in Japan has maintained records of the jellyfish



Table 3. Published reports of jellyfish interfering with aquaculture operations around the world. Species indicated with asterisk (\*) are holoplanktonic; all others have a benthic stage. Pref. = Japanese prefecture

Species	Year (months)	Location	Aquaculture damage	Source
<b>Asia</b>				
<i>Aurelia aurita</i> (s. l.)	1950 (Jul–Sep)	Lake Hachirogata, Akita Pref.	Mass mortality of fish and bivalves	Yasuda (1988)
<i>Porpita porpita</i> *	2000 (Aug–Oct)	Kyoto, Fukui Prefs.	Mortality of penned fish	Yasuda (2003)
<i>Pelagia noctiluca</i> *	2004 (Apr)	Ehime Pref.	Mortality of penned fish	S. Uye (pers. comm. from local fisherman)
<b>Australia/Indo-Pacific</b>				
Unidentified Rhizostome scyphozoan	Before 1995 2006	India Goa, India	Giant tiger prawns Shrimp	Rajagopal et al. (1995) R. A. Sreepada (pers. comm.)
<b>Europe</b>				
<i>Pelagia noctiluca</i> *	1994	Brittany, France	Salmon and trout	Merceron et al. (1995)
<i>Cyanea capillata</i>	1996	Loch Fyne, Scotland	Thousands of salmon killed, GB £ 250 000 loss	Anonymous (1996)
<i>Solmaris corona</i> *	1997, summer	Shetland	Salmon killed	Anonymous (1997a)
<i>Solmaris corona</i> , <i>Phialidium</i> sp., <i>Leuckartiara octona</i> , <i>Catablema vesicarium</i>	2001–02 (Aug)	Isle of Lewis in the Outer Hebrides, Scotland	2 747 680 salmon killed in 11 incidents, GB £ 5 million loss	Johnson (2002)
<i>Apolemia uvaria</i> *	1997–98 (Nov–Feb); 2003	West coast of Norway	Killed salmon; 600 tons killed	Båmstedt et al. (1998), Heckmann (2004)
<b>North America</b>				
<i>Moerisia lyonsi</i>	1970s; 1994–97 (May–Oct)	Mesocosms, Louisiana & Maryland, USA	Killed decapods; ≤13.6 medusae l <sup>-1</sup>	Sandlifer et al. (1974) Purcell et al. (1999a)

biomass cleaned daily from the intake screens, providing a decade-long record of jellyfish abundance (Kaneda et al. 2007). Clogging incidents can cause emergency situations at nuclear power plants (NPPs) and can result in significant power loss and economic damage to affected cities. To prevent clogging events, studies on potential threats of jellyfish and on methods to detect and deflect them from the intakes have been

investigated (Marks & Cargo 1974, Marks 1975, Toda et al. 1995, Azis et al. 2000, Lee et al. 2006).

#### POSSIBLE CAUSES OF JELLYFISH INCREASES

Many changes that have occurred in coastal waters due to human activities could benefit pelagic cnidarian



Fig. 2. Left: *Aurelia aurita* (s. l.) jellyfish clog fishing nets in the Seto Inland Sea, Japan (from Uye & Ueta 2004). Right: *Nemopilema nomurai* jellyfish (maximum diameter 2 m; biomass up to 200 kg) collect in fish set nets in coastal waters of Japan (courtesy of the Chugoku Newspaper)

Table 4. Published reports of jellyfish interfering with power station operations around the world. Locations in Japan unless otherwise stated. Pref. = Prefecture

Species	Year (months)	Location	Effects	Source
<b>Asia</b>				
<i>Aurelia aurita</i> (s. l.)	1960–67	Osaka Bay, Harima Nada, Seto Inland Sea	Power reduction, shutdown	Matsueda (1969)
<i>A. aurita</i> (s. l.)	1962–66 (Apr–Sep)	Tokyo Bay	Power reduction, rotary screen damage	Yasuda (1988), Kuwabara et al. (1969)
<i>A. aurita</i> (s. l.)	1964–68 (Apr–Sep)	Osaka Bay	Power reduction, rotary screen damage	Yasuda (1988)
<i>A. aurita</i> (s. l.)	1971–73 (Jun–Jul)	Aichi Pref.	Power reduction, rotary screen damage	Yasuda (1988)
<i>A. aurita</i> (s. l.)	1971–75 (May–Oct)	Fukui Pref.	Power reduction, rotary screen damage	Yasuda (1988)
<i>A. aurita</i> (s. l.)	1972, (Jul)	Tokyo Bay	Power shutdown in Tokyo area	Yasuda (1988)
<i>A. aurita</i> (s. l.)	1997–2000 (Jun–Sep)	Fukui Pref.	Power reduction	Yasuda (2003)
<i>A. aurita</i> (s. l.)	monitored	Wasaka Bay		Matsumura et al. (2005)
<i>A. aurita</i> (s. l.)	1998–2000	Niigata Pref.	Power reduction	Aoki (pers. comm.)
<i>A. aurita</i> (s. l.)	1998–2002 (Apr–Nov)	Ehime Pref.	Power reduction	H. Takeoka (pers. comm.)
<i>A. aurita</i> (s. l.)	1999	Philippines	Half of country lost power	Anonymous (1999)
<i>A. aurita</i> (s. l.)	Often	China	Uljin Nuclear Power Plant intake screen clogged	Lee et al. (2006)
<i>Rhopilema asamushi</i>	1973 (Aug)	Japan	Power reduction	Yasuda (2003)
<i>Cyanea nozakii</i>	1983–84 (Aug–Nov)	Harima Nada, Seto Inland Sea	Power reduction	Yasuda (2003)
<i>Chrysaora melanaster</i>	1997–2000 (Jun–Sep)	Fukui Pref.	Power reduction	Yasuda (2003)
<b>Europe/Middle East/India</b>				
<i>A. aurita</i>	Unknown	Baltic Sea	Blocking	Möller (1984)
<i>A. aurita</i>	1988	India	Madras Atomic Power Station, blocking, station closure	Rajagopal et al. (1989), Masilamoni et al. (2000)
<i>Crambionella orsini</i>	2002	Gulf of Oman, Persian Gulf	Damage to seawater intake systems of desalination and power plants	Daryanabard & Dawson (in press)
<i>C. orsini</i>	2003 (Apr)	Quatar	Damage to seawater intake systems of liquid natural gas plant	Vaidya (2005)
Unidentified	2006 (May)	Arabian Gulf	Blocked intake screens	Azis et al. (2000)
<b>North America</b>				
<i>Chrysaora quinquecirrha</i>	1960s; 2006 (Jul)	Chesapeake Bay, USA	Calvert Cliffs Nuclear Power Plant, Chalk Point Generating Station, clogged intake pumps and nets	Delano (2006)

and ctenophore populations over fish. Several authors have speculated how some of these factors may contribute to jellyfish blooms (e.g. reviews by Arai 2001, Mills 2001, Purcell et al. 2001b, Parsons & Lalli 2002, Oguz 2005a,b, Purcell 2005, Graham & Bayha 2007). We do not believe it is necessary to detail the cases previously reviewed, and refer the reader to the appropriate reviews and discuss additional information. We will consider how climate change, eutrophication, fishing, aquaculture, construction, species invasions and the co-occurrence of many of these factors may enhance populations of gelatinous species. We emphasize that these possible anthropogenic contributions to blooms of gelatinous species have not actually been demonstrated to cause any blooms; the inferences are from apparent correlations.

### Climate change

Existing long-term data have shown fluctuations of pelagic cnidarian and ctenophore abundance that are correlated with environmental variables (reviewed Purcell 2005). The majority of moderate-temperature species studied (18 of 24) have been reported to increase in warm temperatures (Table 5). Abundance data for *Aurelia aurita* (s. l.) and *Nemopilema nomurai* in Asia have not been analyzed against climatic variables; however, temperatures in the Seto Inland Sea (*A. aurita*) and in the Yellow Sea, where blooms of *N. nomurai* may originate, have increased in recent decades (Uye & Ueta 2004, Uye in press). Climate indices, such as the North Atlantic Oscillation (NAO) Index, have been correlated with jellyfish abundances

Table 5. Analyses of long-term records of jellyfish, siphonophore and ctenophore populations and their responses to ocean warming. Early/late and long/short: change in seasonal timing and duration; more/fewer: changes in abundance; H: high; L: low; +: positive; -: negative; fw: freshwater; sun: solar insolation; NAO: North Atlantic Oscillation; nd: not reported, no data available. Species indicated with asterisk (\*) are holoplanktonic; all others have a benthic stage. Pref. = Prefecture

Species	Location	Response to warming	Other favorable conditions	Dates (no. of years)	Source
<b>Scyphomedusae</b>					
<i>Aurelia aurita</i> (s. l.)	Seto Inland Sea, Japan	More	nd	1983–2003 (20)	Uye & Ueta (2004)
<i>Nemopilema nomurai</i>	Japan Sea	More	nd	1920, 1958, 1995, 2002–05 (85)	Uye (in press)
<i>Mastigias</i> sp.	Jellyfish Lake, Palau	Fewer	<34°C, 25 < salinity < 40	1980–99 (20)	Dawson et al. (2001)
<i>Pelagia noctiluca</i> *	Mediterranean Sea	More	H salinity, + atmospheric pressure	1885–1985 (100)	Goy et al. (1989), Molinero et al. (2005)
<i>A. aurita</i> , <i>Cyanea capillata</i> , <i>C. lamarckii</i>	North Sea	Fewer	- NAO	1966–93 (27) 1971–86 (15)	Lynam et al. (2004)
<i>Chrysaora quinquecirrha</i>	Chesapeake Bay, USA	More, early	L fw input, H salinity, H sun, - NAO	1960–95 (35)	Cargo & King (1990), Purcell & Decker (2005)
<i>Chrysaora melanaster</i>	Eastern Bering Sea	More	Moderate ice cover & current	1975–2005 (30)	Brodeur et al. (in press)
<i>Chrysaora fuscescens</i>	Oregon, USA	Fewer	Upwelling, cold, H salinity	2000 & 2002 (2)	Suchman & Brodeur (2005)
<b>Hydromedusae</b>					
<i>Liriope tetraphylla</i> *	Mediterranean Sea	More	H salinity; climate indices	1966–93 (27)	Buecher et al. (1997), Molinero et al. (2005)
<i>Rhopalonema velatum</i>	Mediterranean Sea	More	Climate indices	1966–93 (27)	Molinero et al. (2005)
<i>Solmundella bitentaculata</i>	Mediterranean Sea	More	Climate indices	1966–93 (27)	Molinero et al. (2005)
<i>Aglantha digitale</i> *	Greenland	More	H salinity	1950–68 (18)	Pedersen & Smidt (2000)
<i>A. digitale</i> *, <i>Bougainvillia</i> spp., <i>Leuckartiara octona</i> , <i>Obelia</i> spp., <i>Clytia hemispherica</i>	North Sea	Early, long	nd	1974–94 (20)	Greve et al. (2001)
<i>Mitrocoma cellularia</i>	Monterey Bay, USA	More	H salinity	1990–98 (8)	Raskoff (2001)
<i>Colobonema sericeum</i> *	Monterey Bay, USA	Fewer	L salinity	1990–98 (8)	Raskoff (2001)
<i>Aequorea victoria</i>	Vancouver Island, Canada	More	H salinity	1983–87 (5)	Purcell (2005)
<b>Siphonophores</b>					
<i>Chelophyes appendiculata</i> *, <i>Abylopsis tetragona</i> *	Mediterranean Sea	More	H salinity	1966–95 (29)	Buecher (1999)
<b>Ctenophores</b>					
<i>Pleurobrachia pileus</i> *, <i>Beroe</i> spp.*	North Sea	Early, long	nd	1974–94 (20)	Greve et al. (2001)
<i>Pleurobrachia rhodopsis</i> *	Mediterranean Sea	Less	Climate indices	1966–93 (27)	Molinero et al. (2005)
<i>Mnemiopsis leidyi</i> *	Narragansett Bay, USA	Early, long, more	nd	1950, 1971–99 (49)	Sullivan et al. (2001)



instead of, or in addition to, environmental measurements (e.g. Lynam et al. 2004, 2005, Molinero et al. 2005). Global temperatures are expected to rise 0.2°C during the next 2 decades (IPCC 2007). Warming of the oceans may increase many populations of gelatinous species and also shift the population distributions poleward, as seems to be occurring for the ctenophore *Mnemiopsis leidyi* (Sullivan et al. 2001, Faase & Bayha 2006, Hansson 2006). By contrast, warming may be detrimental to species living near their thermal maxima, as for *Mastigias* sp. in Palau (Dawson et al. 2001). In addition to changes in population size and distribution, warming will alter the timing and duration of the pelagic stages.

Only 7 species have been reported not to increase their numbers with warming (Table 5). The population of tropical *Mastigias aurita* jellyfish (but not *Aurelia* sp. [s. l.] jellyfish) in the very stable environment of Jellyfish Lake, Palau, was nearly eliminated during high temperature and salinity conditions of an El Niño (Dawson et al. 2001). While one meroplanktonic hydromedusan species increased during an El Niño, a holoplanktonic species did not (Raskoff 2001). *Chrysaora fuscescens* were most abundant at stations having cold (8 to 10°C), saline water (>33.8) along the US North Pacific coast, although they were sampled over wide ranges of temperature (7.7 to 14°C) and salinity (30.1 to 34) (Suchman & Brodeur 2005). Jellyfish of another species, *C. melanaster*, increased in the Bering Sea with warming from the shift to a positive Pacific Decadal Oscillation (PDO) in 1976 to 1977, increasing most dramatically in the 1990s, but then decreasing with further warming since 2000 (Brodeur et al. in press); *C. melanaster* jellyfish in the Gulf of Alaska also increased after 1976 to 1977, but have not decreased recently (Litzow 2006). The climate shift in 1998 to 1999 did not return the PDO to a negative state (Litzow 2006).

Climate effects on jellyfish in the North Sea also contrast with the general trend of more jellyfish and ctenophores in warm conditions. Lynam et al. (2004) stated the jellyfishes, *Aurelia aurita*, *Cyanea capillata* and *Cyanea lamarckii*, were negatively correlated with the NAO Index (no temperature data provided) during 1971 to 1986 in the North Sea. A cold event occurred between 1978 and 1982 that was related to decreased inflow of warm Atlantic water, increased inflow of cold, deep Norwegian water and arctic-boreal plankton, and abundant *A. aurita* and *C. lamarckii* jellyfish. Lynam et al. (2005) analyzed the same data by region and showed that the NAO correlations switched sign in northern parts of the study area, but high jellyfish abundance was consistently associated with cool conditions. A different study used Continuous Plankton Recorder (CPR) data on nematocyst occurrence as an

index of jellyfish abundance in the North Sea during 1958 to 2000 (Attrill et al. 2007); nematocysts were positively correlated with the NAO Index, but not with temperature, and the Lynam et al. (2004) data fit into the longer-term positive NAO Index trend. Both studies discuss the fact that the trends depend on the region of the North Sea and on the current regime. With continued climate warming, the NAO is predicted to move into a stronger positive phase (Osborn 2004), which according to Attrill et al. (2007) would lead to a greater abundance of jellyfish. Further study of jellyfish in the North Sea and clarification of the sources of nematocysts in CPR samples seem necessary to resolve these apparently conflicting results.

Other studies have shown that blooms of pelagic cnidarians often are associated with changes in current patterns, which may cause incursions or retention of pelagic cnidarians, as for *Pelagia noctiluca* in the Adriatic Sea (UNEP 1984, 1991, Purcell et al. 1996b) and the siphonophores, *Muggiaea atlantica* in the German Bight and *Apoemia uvaria* off Norway, as discussed by Mills (2001). High abundances of gelatinous species in the Mediterranean Sea also have been associated with variations in water mass and high salinity as well as warm temperature (UNEP 1984, 1991, Goy et al. 1989, Buecher 1999, Molinero et al. 2005) (Table 5). A large bloom of the scyphomedusa, *Phyllorhiza punctata*, in the northern Gulf of Mexico in 2000 (Graham et al. 2003) may have resulted from advection of jellyfish from the Caribbean Sea by the northerly Loop Current (Johnson et al. 2005). Some blooms resulting from current intrusions have been single events (e.g. as for *M. atlantica*, *A. uvaria*, *P. punctata*), while others occur repeatedly and persist for years with climate-driven current variations (as for *P. noctiluca* and the North Sea species discussed previously). With changing climate, current patterns also are expected to change (IPCC 2007), which may result in blooms in new locations. Concentrations of jellyfish may occur nearshore due to interactions between water flow and jellyfish behavior (reviewed by Graham et al. 2001, see also Suchman & Brodeur 2005).

Environmental factors may directly affect the size and timing of jellyfish populations. For *Pelagia noctiluca*, a scyphomedusan lacking a benthic stage, ephyrae did not develop at 4.5°C and took twice as long to develop at 13.5 than at 19°C (Avian 1986). In temperate scyphozoans and hydrozoans, warm temperatures increased the asexual production of buds and new jellyfish, and the ratio of jellyfish to polyps in the 3 species studied (*Aurelia labiata*, *Chrysaora quinquecirrha* and *Moerisia lyonsi*; reviewed in Purcell 2005). Both temperature and salinity had significant effects and strong interaction (Purcell 2007). Substantial increases were calculated in the numbers

of jellyfish produced by the benthic polyps (up to 24 % per 1°C increase and 28 % per ppt salinity change) and in the acceleration of jellyfish production (up to 6.6 d per 1°C increase and 2.0 d per ppt salinity change) (Table 6). We know of no similar published studies on arctic or tropical species, or on ctenophores or siphonophores.

Increased light also accelerated strobilation in *Chrysaora quinquecirrha* and *Aurelia labiata* (in Loeb 1973, Purcell in press), but to our knowledge has been tested only for these scyphozoans. Synchronized production with seasonally changing factors, such as temperature and light, possibly is universal among pelagic cnidarians, but few species have been tested.

Changes in temperature and salinity also can affect pelagic cnidarian and ctenophore populations by changes in ocean productivity (Behrenfeld et al. 2006), but the results of such changes are difficult to predict since they must translate up through the food web and will differ by location. Various authors have suggested that increased stratification related to warming and the resulting recycled production might favorably affect jellyfish populations. Reduced jellyfish populations occurred during years with low productivity in unusually warm conditions in the Bering Sea (Brodeur et al. in press). High nematocyst occurrences in CPR samples were correlated with high productivity (as indicated by the Phytoplankton Colour Index) in the North Sea (Attrill et al. 2007). Clearly, abundant food is advantageous for all gelatinous species.

Table 6. *Aurelia labiata*, *Chrysaora quinquecirrha* and *Morisia lyonsi*. Percentage increases in no. of jellyfish produced (Incr.) and no. of days production would be accelerated (Accel.) per 1°C temperature increase and per 1 ppt salinity increase (modified from Purcell in press). na = not available

Species and experiment (salinity or temperature)	Range tested (°C/ppt)	Incr. (%)	Accel. (d)
<b>Temperature</b>			
<i>A. labiata</i> (20–34)	7–15	11.3	4.24
<i>A. labiata</i> (27)	10–15	8.8	6.57
<i>A. labiata</i> (27)	15–20	0.4	0.30
<i>C. quinquecirrha</i> (5–20)	15–25	5.3	1.40
<i>C. quinquecirrha</i> (20–35)	15–20	18.4	1.40
<i>C. quinquecirrha</i> (20–35)	20–25	0.7	1.40
<i>M. lyonsi</i> (5–25)	20–29	24.4	1.15
<b>Salinity</b>			
<i>A. labiata</i> (7–15°C)	20–27	3.2	1.95
<i>A. labiata</i> (7–15°C)	34–27	3.7	0.81
<i>C. quinquecirrha</i> (15–25°C)	5–20	6.7	na
<i>C. quinquecirrha</i> (15–25°C)	35–20	5.7	na
<i>M. lyonsi</i>	15–5	0.7	0.08
<i>M. lyonsi</i> (20–29°C)	25–15	28.2	0.82

One major repercussion of increasing CO<sub>2</sub> concentrations in the atmosphere is decreasing pH of ocean waters, which has been reported widely (e.g. Caldeira & Wickett 2003). Optimal pH for *Rhopilema esculenta* jellyfish was 7.9 to 8.5, with some reduction in swimming and feeding at 9.0 < pH < 7.4, and a marked reduction at 9.5 < pH < 6.5 (Gu et al. 2005), which suggests considerable tolerance for changes in pH; however, pH effects have rarely been tested on gelatinous species. Attrill et al. (2007) showed a significant positive correlation of nematocyst occurrence in CPR samples with decreasing pH (range 8.0 to 8.3) during 1971 to 1995, and speculated that non-calcifying gelatinous organisms might benefit from detrimental effects of low pH on calcifying organisms. Ocean acidification could have serious consequences for organisms that build skeletons or shells of calcium carbonate (CaCO<sub>3</sub>) such as pteropods (Orr et al. 2005). Many jellyfish have microscopic calcium statoliths that serve in orientation; in scyphomedusae and cubomedusae, the statoliths are composed of calcium sulfate hemihydrate (CaSO<sub>4</sub> × ½ H<sub>2</sub>O), and in the hydromedusae the statoliths (absent in Anthomedusae) are calcium magnesium phosphate (reviewed in Becker et al. 2005, Tiemann et al. 2006). Ctenophores have MgCaPO<sub>4</sub> concretions (Chapman 1985). Ocean pH is predicted to decrease by 0.3 during the 21st century (IPCC 2007); however, the effects of decreasing pH on statolith secretion by jellyfish are unknown (V. J. Fabry pers. comm.).

### Cultural eutrophication

Eutrophication is considered to be one of the major global pollution problems (e.g. Howarth 2002). Eutrophication is associated with increased nutrients, altered nutrient ratios and increased turbidity where humans develop coastal areas. Most simply, increased nutrients often lead to greater biomass at all trophic levels (e.g. Daskalov 2002). More food for polyps and jellyfish increases asexual production of jellyfish (e.g. Purcell et al. 1999a, Stibor & Tokle 2003) and sexual reproduction (Lucas 2001). In her review, Arai (2001) could not positively identify the cause of jellyfish blooms to be nutrient increases, which co-occurred with several other environmental changes.

Since Arai's (2001) review increases in jellyfish populations have been attributed to excessive nutrient additions from human sources in additional areas. Nutrients in the Yangtze River estuary have increased (Zhang et al. 1999) with greatly increased uses of nitrogen fertilizers after the 1970s (Glibert et al. 2005) and may be related to recent jellyfish blooms there. Agriculture and development increased nitrate levels

10-fold in the Mar Menor, Spain, while wastewater treatment decreased phosphate by one-tenth; these conditions were associated with annual blooms of 2 rhizostome scyphomedusae, *Cotylorhiza tuberculata* and *Rhizostoma pulmo*, since 1993 (Pérez-Ruzafa et al. 2002). These examples suggest that high nitrogen ratios may favor jellyfish blooms. Other modifications of these coastal environments have also occurred, and are discussed below in 'Construction'.

Eutrophication also causes complex changes in the food web. Greve & Parsons (1977) first hypothesized 2 parallel food paths in the oceans, a diatom-based path that ends with large consumers having 'high energy' requirements (e.g. whales), and a flagellate-based path that ends with 'low energy' consumers (e.g. jellyfish). Shifts from the diatom- to the flagellate-based path could result from pollution, eutrophication or climate changes. This hypothesis has been elaborated over time (Smayda 1993, Parsons & Lalli 2002, Sommer et al. 2002). Sommer et al. (2002) proposed 3 types of nutrient regimes: (1) upwelling systems, with high ratios of silica (Si) to nitrogen (N) and phosphate (P) plus diatoms and flagellates; (2) oligotrophic oceanic systems with low nutrients and predominated by picoplankton (5 to 10  $\mu\text{m}$ ); and (3) eutrophicated coastal systems, with elevated N and P and summer blooms of inedible algae (often large dinoflagellates). High N:P ratios shift the phytoplankton community away from diatoms towards flagellates and jellyfish (Nagai 2003). Eutrophication also is connected with size reduction of the zooplankton community (Uye 1994); the zooplankton in eutrophic Tokyo Bay is almost entirely very small *Oithona davisae* copepods, which primarily feed on small flagellates (Uchima 1988). Thus, nutrient enrichment may change the lower trophic structure towards a microplankton-based food web. This size-reduction of the lower trophic levels is thought to be detrimental to fish, most of which are visual predators that prefer large zooplankton, thereby benefiting jellyfish, which are not visual and consume small as well as large prey.

There are also top-down effects that determine the microplankton community composition. Both Smayda (1993) and Sommer et al. (2005) emphasize the importance of selective grazing by copepods, but previous discussions have not fully appreciated the role of selective feeding by the jellyfish predators (e.g. Purcell 1997) in modifying the microplankton community. First, zooplankton predation by jellyfish will alter the grazer composition, which changes the microplankton (e.g. Behrends & Schneider 1995). Second, grazing by jellyfish on microzooplankton tends to be forgotten; however, it has been demonstrated for young ctenophores and jellyfish (e.g. Stoecker et al. 1987a,b, Olesen et al. 1996), which ate ciliates, but not dinoflagel-

lates. Major beneficiaries of eutrophic waters appear to be *Aurelia aurita* jellyfish, whose complex surface-ciliary feeding method was detailed by Southward (1955). Recent stable isotope analyses place *A. aurita* (s. l.) at a slightly higher trophic level than copepods, confirming this jellyfish's utilization of microplanktonic foods (Kohama et al. 2006, R. D. Brodeur et al. unpubl.). *Aurelia* spp. jellyfish, in particular, frequent highly eutrophic waters (Ishii 2001, Mills 2001, Nagai 2003). A hydromedusan species, *Aglaura hemistoma*, recently was found to eat protozoans (Colin et al. 2005). The diets of related species (*Proboscoidactyla flavicirrata*, small *Aglantha digitale*) contain mainly prey that swim by cilia (rotifers, veligers) (reviewed by Purcell & Mills 1988); both *Aglaura* and *Aglantha* are in the same family of the Suborder Trachymedusae and feed using ciliary currents (as in Colin et al. 2005); thus, related species also may eat microplankton. Jellyfish also take up dissolved organics, but as emphasized by Arai (2001), study of such uptake has been neglected. We conclude that some gelatinous species may be particularly suited to flourish in environments with microplankton-based food webs.

In terms of nutrient cycling gelatinous species excrete and take up dissolved organic matter. The uptake of dissolved organics by jellyfish or ctenophores seldom has been studied, but studies on nitrogen excretion are numerous (e.g. Schneider 1989, Pitt et al. 2005). When in high abundances, gelatinous species may contribute significantly to nitrogen and phosphate budgets. The importance of decomposition of jellyfish following blooms and the contribution to benthic communities has only recently been investigated (Billet et al. 2006, Rieman et al. 2006, Titelman et al. 2006).

Eutrophication often is associated with low dissolved oxygen levels (hypoxia), especially in the bottom waters (e.g. Breitburg et al. 2003). Fish avoid, or die in, waters of  $\leq 2\text{--}3\text{ mg O}_2\text{ l}^{-1}$  (reviewed in Breitburg et al. 2001), but many jellyfish species are tolerant of  $\leq 1\text{ mg O}_2\text{ l}^{-1}$  (reviewed in Purcell et al. 2001b). Subsequent to that review the hypoxia tolerance of several estuarine jellyfish, including *Aurelia labiata*, and ctenophores were reported to have great tolerance of low dissolved oxygen (Rutherford & Thuesen 2005, Thuesen et al. 2005). Jellyfish polyps are also tolerant of low oxygen (Condon et al. 2001) and may find additional habitat where other epifauna is reduced in hypoxic waters (Ishii 2006). Some species of jellyfish (and planktonic ctenophores) lack a polyp stage, and those species may persist where hypoxic bottom waters prevent others with vulnerable benthic stages (Arai 2001). Loss of species with a benthic stage was suggested to explain the reduction of hydromedusan species from over 40 in 1910 to fewer than 20 since 1972 (Benović et al. 2000).

Pelagic cnidarian and ctenophore predation on zooplankton may reduce grazing on phytoplankton, which in turn could increase the flux of ungrazed phytoplankton to the benthos and reinforce hypoxia. This was tested in Chesapeake Bay in 1987 to 1990 when scyphomedusae predominated, but predation was insufficient to reduce zooplankton (Purcell et al. 1994); the same area was examined from 1996 to 2000 when ctenophores predominated and their predation did reduce zooplankton densities during that period (Purcell & Decker 2005). The positive reinforcement of hypoxia by gelatinous species may be important in coastal waters (see also Møller & Riisgård 2007).

Eutrophication and development reduce water clarity and light penetration, which may alter the feeding environment to benefit gelatinous predators over fish. Epipelagic fish are visual feeders, while jellyfish are non-visual; turbid water could reduce feeding by fish, but not affect jellyfish. Eiane et al. (1997, 1999) compared the optical properties of water in Norwegian fjords; jellyfish (i.e. *Periphylla periphylla*) predominate in Lurefjorden, which has much greater light absorbance than other fjords with fish. The reduced light penetration in Lurefjorden was due to coastal water influence, not to eutrophication or development. To our knowledge this study is the only test of a possible advantage of reduced visibility to jellyfish.

### Fishing

Fishing may positively affect pelagic cnidarian and ctenophore populations by removing predators of the gelatinous species (reviewed in Purcell & Arai 2001, Arai 2005). Gelatinous species are eaten by many species of fish, some of which are commercially important, such as chum salmon *Onorhynchus keta*, butterfish *Pepilus triacanthus*, and spiny dogfish *Squalus acanthias* (Arai 1988, 2005, Purcell & Arai 2001). The occurrence of ctenophores in spiny dogfish stomachs was used to infer a major increase in ctenophore populations between 1981 and 2000 along the northwest Atlantic shelf (Link & Ford 2006). Populations of other predators have been reduced at least in part because of fishing activities. Leatherback turtles *Dermodochelys coriacea* have decreased dramatically in the Pacific Ocean (Spotila et al. 2000) and are believed to eat primarily gelatinous prey (see Arai 2005, Houghton et al. 2006); other sea turtle species also eat jellyfish to some degree and also are at risk.

Fishing for zooplanktivorous forage fish species removes potential competitors of gelatinous predators. Diets of forage fishes and gelatinous species overlap (Purcell & Sturdevant 2001, R. D. Brodeur et al. unpubl.); therefore, reduction of forage fish can pro-

vide additional food for gelatinous predators. Mills (2001) suggested that increases in the siphonophore *Nanomia cara* in the Gulf of Maine could be due to reduction of zooplanktivorous fish species there. Reduction of zooplanktivorous fish populations was implicated when ctenophores and jellyfish replaced fish in the Black Sea and the Benguela Current (Shiganova 1998, Daskalov 2002, Oguz 2005b, Lynam et al. 2006). Overharvest of mollusks and crustaceans also can lead to dramatic changes in ecosystems (in Jackson et al. 2001). Overfishing is considered to be a severe problem (e.g. Pauly & Watson 2003). Jackson et al. (2001) and Daskalov et al. (2007) discuss how overfishing of one resource after another, in combination with other ecosystem damage, may lead to greater jellyfish and ctenophore populations.

### Aquaculture

Aquaculture may unintentionally benefit jellyfish populations in several ways. First, if additional feed is provided, eutrophication of the waters can result in those consequences previously discussed. Second, the culture structures provide additional substrate on which the benthic stages may live and produce more jellyfish. The effects of aquaculture on an *Aurelia aurita* population were illustrated in Tapong Bay, Taiwan, where oysters and fish were extensively cultured before Jan 2003 (Fig. 3). Jellyfish were abundant during sampling between Apr 1999 and May 2002; however, they were absent after removal of the culture rafts (Fig. 4). Analysis suggested that the aquaculture structures had provided shaded substrate for the

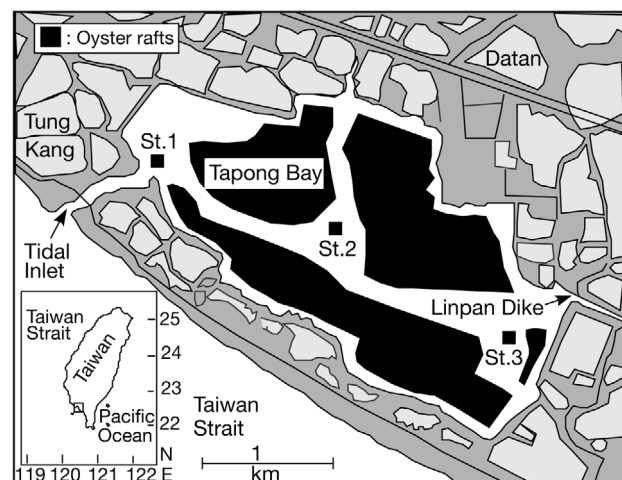


Fig. 3. Tapong Bay in southwestern Taiwan with surrounding fish culture ponds (light gray) and oyster culture rafts (black areas in bay) before 2003. All oyster rafts were removed by 2003. Solid squares (■) mark 3 sampling stations



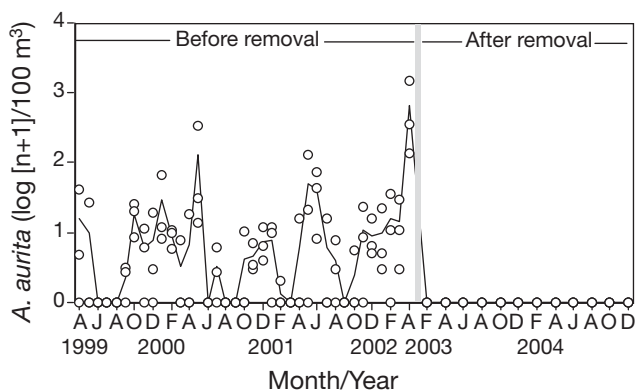


Fig. 4. *Aurelia aurita*. Abundance of jellyfish at 3 stations in Tapong Bay, Taiwan, which had extensive oyster culture rafts before January 2003 (grey line: removal date)

polyps and retention in the lagoon (Lo et al. in press). Another unintended benefit for gelatinous predators is that forage fish (e.g. anchovies, sardines and menhaden) are harvested for fish meal for aquaculture feed (e.g. Kristofersson & Anderson 2006) and removal of zooplanktivorous fish may provide opportunities for their gelatinous competitors' population growth, as discussed in the previous section.

Aquaculture also intentionally enhances jellyfish populations. In response to a dramatic decline in catches of the preferred edible jellyfish, *Rhopilema esculentum*, China initiated an aquaculture program in 1983 (Xu et al. 1997, Liu & Bi 2006). One hundred million 1 cm jellyfish are released annually in February and March, and by August they reach 50 cm in length. The cost:benefit ratio ranged from 1:2 to 1:4. Because of the success of Chinese jellyfish aquaculture and the resultant fishery, Malaysia began a similar program in 2004 and plans another center (Anonymous 2004). Such jellyfish enhancement programs seem certain to have ecological repercussions that are unstudied.

### Construction

We use the term 'construction' for a variety of human disturbances to aquatic habitats that have either added structures to or altered the characteristics of coastal waters. In addition to aquaculture (as discussed in the last section), humans add many other structures to coastal waters including docks, marinas, breakwaters, oil platforms and artificial reefs, all of which provide surfaces for polyps, but the importance of this is unknown.

Most reported jellyfish blooms have occurred in heavily populated areas surrounding semi-enclosed water bodies. Such areas often have extensive construction in addition to eutrophication and fishing, and

the effects are impossible to separate (Arai 2001). In China the Three Gorges Dam on the Yangtze River became operational in 2003; downstream changes in the estuary have included an earlier seasonal influx of high salinity water and jellyfish blooms, including one of a newly introduced species (Xian et al. 2005). Eutrophication also is a serious problem in China (Zhang et al. 1999). These hydrological alterations may affect the Yellow Sea, where *Nemopilema nomurai* blooms may originate. Changes in water flow to the Black Sea were suggested to contribute to changes favoring jellyfish and ctenophores (e.g. Oguz 2005b). Jellyfish blooms have become problematic in the Mar Menor, Spain, where the inlets to the lagoon were enlarged, reducing salinities from 50–52 to 43–47; in addition, extensive development (including dredging and beach construction) changed 42% of the shoreline, and eutrophication (discussed previously) has been extensive (Pagés 2001).

Nuclear and thermal power plants often use coastal waters for cooling and discharge the heated water back into the marine environment. The plume from the Daya Bay NPP, China, extends 8 to 10 km and increases temperatures by 1 to 1.5°C (Tang et al. 2003). China and Korea have 4 NPPs in or near the Yellow Sea, a possible source of *Nemopilema nomurai* blooms. The Quinshan NPP started commercial operation in 1994 (INSC 2007); problem jellyfish blooms (*Aequorea* sp., *Cyanea* sp., *Sanderia* sp., *Stomolophus meleagris*) in that region (Yangtze River plume) began in the mid 1990s and have been increasing (Cheng et al. 2005). The Quinshan NPP has 1 operational reactor, with 2 more under construction (INSC 2007); hence, additional changes may be anticipated.

### Alien invasions

Several species of jellyfish have been accidentally introduced in many locations around the world (Table 7); some have been introduced in many places (Dawson et al. 2005), and some have caused tremendous ecosystem disruptions and economic losses (reviewed in Graham & Bayha 2007). The transport between locations has mostly been via ballast water, and sometimes from the aquarium trade (Bolton & Graham 2006). Newly introduced species often display large initial blooms that become less intense; however, the stage is set for subsequent large blooms when fortuitous conditions prevail, and for expansion of the population into new areas. *Rhopilema nomadica* first appeared in the Mediterranean in the mid-1970s and now is found along all coastlines of the eastern Mediterranean Sea (reviewed in Graham & Bayha 2007). In the early 1980s, the infamous ctenophore, *Mnemiopsis*



Table 7. Species of jellyfish and ctenophores known to have been inadvertently introduced to non-native habitats. Species indicated with asterisk (\*) are holoplanktonic; all others have a benthic stage

Invading species	Areas of invasion	Source
<b>Scyphomedusae</b>		
<i>Aurelia</i> spp.	Multiple invasions	Dawson et al. (2005)
<i>Rhopilema nomadica</i>	Eastern Mediterranean Sea	Reviewed in Graham & Bayha (2007)
<i>Phyllorhiza punctata</i>	Western Australia, Hawaii & San Diego, USA, Caribbean and Mediterranean seas, Gulf of Mexico	Reviewed in Graham et al. (2003), Bolton & Graham (2004), Graham & Bayha (2007)
<i>Cassiopea andromeda</i>	Hawaii and Mediterranean Sea	Reviewed in Graham & Bayha (2007)
<i>Sanderia malayensis</i>	Yangtze River estuary	Xian et al. (2005)
<b>Hydromedusae</b>		
<i>Craspidacusta sowerbii</i>	Fresh water, all continents except Antarctica	Dumont (1994)
<i>Moerisia lyonsi</i>	Chesapeake and San Francisco bays, and Lake Ponchatrain, USA	Reviewed in Purcell et al. (1999a)
<i>Blackfordia virginica</i>	San Francisco Bay	Mills & Sommer (1995)
<i>Maeotias inexpectata</i>	San Francisco Bay	Mills & Sommer (1995)
<b>Ctenophores</b>		
<i>Mnemiopsis leidyi</i> *	Black, Azov, Caspian, Mediterranean and North seas	Reviewed in Graham & Bayha (2007)
<i>Beroe ovata</i> *	Black Sea	Reviewed in Graham & Bayha (2007)

*leidyi*, first invaded the Black Sea, where it spread to the Sea of Azov and the Mediterranean and Caspian seas (e.g. Purcell et al. 2001c, Graham & Bayha 2007); recent appearance of *M. leidyi* in the North Sea appears to be a separate introduction and has spread to the Baltic Sea (Faasse & Bayha 2006, Hansson 2006). Thus, blooms may occur in areas where the species did not previously occur.

### Multiple interacting factors

Most of the problem jellyfish blooms have several probable contributing causes (Table 8). For example, in Chinese waters jellyfish blooms have followed warming, extensive eutrophication, fishing, construction and invasion. Jellyfish blooms followed extensive habitat modification in the Mar Menor, Spain, where in addition to eutrophication and construction (discussed previously), the bottom habitat changed from sand to mud, the algal invader *Caulerpa prolifera* replaced sea grasses, oysters were introduced providing additional

Table 8. Summary of possible contributing factors to major jellyfish blooms around the world. Species indicated with asterisk (\*) are holoplanktonic; all others have a benthic stage. + = probable, ? = unknown or not examined, - = unlikely

Bloom location	Main species	Possible factors contributing to bloom					Source
		Climate	Eutrophication	Fishing	Aqua-culture	Construction	
Tokyo Bay, Seto Sea	<i>Aurelia aurita</i> (s. l.)	+	+	+	+	+	Ishii (2001), Uye & Ueta (2004)
East Asian marginal seas	<i>Nemopilema nomurai</i>	+	+	+	?	+	Uye (in press)
Yangtze River estuary	<i>Aequorea</i> sp., <i>Cyanea</i> sp., <i>Sanderia malayensis</i>	+	+	+	?	+	Ding & Cheng (2005), Cheng et al. (2005), Xian et al. (2005)
Black Sea	<i>Mnemiopsis leidyi</i> *	+	+	+	-	+	Oguz (2005a,b)
Mar Menor	<i>Cotylorhiza</i> , <i>Rhizostoma</i>	?	+	+	+	+	Pagés (2001)
Mediterranean and Adriatic seas	<i>Pelagia noctiluca</i> *	+	-	+	-	-	Goy et al. (1989), Purcell et al. (1999b)
Benguela Current	<i>Chrysaora hysoscella</i> , <i>Aequorea forskalea</i>	?	-	+	-	-	Lynam et al. (2006)
Chesapeake Bay	<i>Chrysaora quinquecirrha</i> , <i>Mnemiopsis leidyi</i> *	+	+	+	-	-	Purcell & Decker (2005)
Bering Sea	<i>Chrysaora melanaster</i>	+	-	+	-	-	Brodeur et al. (in press)
Lurefjorden	<i>Periphylla periphylla</i> *	?	-	?	-	-	Eaine et al. (1999)

substrate for the jellyfish polyps, bottom waters became hypoxic, and once vigorous fisheries declined (Pagés 2001). The great success of the introduced ctenophore, *Mnemiopsis leidyi*, in the Black Sea was probably due to many factors, including previous ecosystem damage (reviewed in Oguz 2005a,b), overfishing (e.g. Shiganova 1998, Daskalov 2002), climate variations (e.g. Oguz 2005a) and the initial absence of a controlling predator (Purcell et al. 2001c). Subsequently, the *M. leidyi* population was controlled by the invasion of a predator, the ctenophore, *Beroe ovata* (e.g. Oguz 2005a). In the Bering Sea a general additive modeling (GAM) analysis of the increase in the 1980s and 1990s and abrupt decrease after 2000 of *Chrysaora melanaster* jellyfish revealed that abiotic factors (moderate temperature, low to moderate ice cover, low spring mixing, low current flow) and biotic factors (high jellyfish biomass the previous year, low to moderate abundance of walleye pollock *Theragra chalcogramma*) all favored high jellyfish biomass (Brodeur et al. in press). Degraded habitats may promote persistent blooms of gelatinous species.

## DISCUSSION

### Potential for problems with jellyfish to increase in the future

Long-term changes in climate have been documented, such as increased temperatures and decreased ice in the Arctic, changes in precipitation, ocean salinity, wind patterns and extreme weather frequency and intensity; it is considered 'virtually certain' that these changes will continue in the 21st century (IPCC 2007). Global warming is predicted to cause a temperature increase of 0.1 to 0.2°C per decade and ocean surface temperatures will rise nearly everywhere (IPCC 2007). The century long pattern of increasing cloud cover and decreasing light before the 1990s seems to have reversed recently (Wild et al. 2005). There is a high degree of uncertainty in predicting specific changes in many important factors (e.g. precipitation, salinity, currents, cloudiness, production, pH) and the consequences for organisms, because of hydrographic and seasonal variation, and of interactions and feedbacks among the multiple factors, as well as many direct human effects (e.g. Harley et al. 2006, IPCC 2007). For example, the food available to pelagic cnidarians and ctenophores would depend on their competitors and predators (e.g. fish) as well as production. Nonetheless, changes in temperature, salinity, currents and light are very likely to cause changes in the population sizes, distributions and timing of gelatinous species.

To understand how climate variables affect the various species, predictive equations and models using environmental data and climate indices need to be developed, as for *Pelagia noctiluca*, *Chrysaora quinquecirrha*, *C. melanaster* and *Aurelia labiata* (Goy et al. 1989, Cargo & King 1990, Lynam et al. 2004, Attrill et al. 2007, Decker et al. 2007, Brodeur et al. in press, Purcell in press). Combinations of field and laboratory studies also are necessary. It is important to remember that environmental changes will affect both the benthic and pelagic stages of the cnidarians. Even less is known about the benthic stages than the pelagic jellyfish. Basic information, such as polyp habitat, is unknown for most species. To understand the factors affecting jellyfish blooms, it is essential to learn more about the ecology of the benthic stages.

The current world human population is projected to increase 46% by 2050 (US Census Bureau 2006). Human influences and demands on the ocean will increase along with population. Increased demands for energy will drive more dam and power plant construction with associated warming and salinity changes in coastal waters. For example, China has 3 operative nuclear power stations and 4 are under construction (INSC 2007). Increased fertilizer use, particularly in Asia, may cause dissolved inorganic nitrogen exports to the coastal oceans to more than double by 2050 (Seitzinger et al. 2002). Zhang et al. (1999) indicated that the N:P ratio in the Yangtze River would be 300 to 400:1 by 2010, although the 'normal' Redfield N:P ratio is 16:1. Studies on the effects of eutrophication and hypoxia on jellyfish and ctenophores are needed. Whether gelatinous species actually do best in stratified waters with recycled nutrients and small planktonic foods needs to be determined. Global fish production is projected to double between 1997 and 2020, with especially large increases occurring in developing nations and in aquaculture (Delgado et al. 2003). Much of the extremely valuable long-term data on jellyfish populations are from fisheries. Quantification of jellyfish live catch volume and numbers should become standard protocol in fisheries surveys. Contrary to nearly all past research in which jellyfish and fish are studied separately, future work should consider them together (e.g. Brodeur et al. in press, Suchmann & Brodeur 2005).

A larger human population brings increased coastal development, aquaculture and commerce, with enhanced opportunities for polyp settlement and alien species introduction. Global bivalve (mussels, oysters, scallops) and marine fish aquaculture have increased dramatically in recent decades, especially in Asia (Fig. 5) (FAO 2007), and can provide favorable habitat for jellyfish polyps. Research to determine materials

that reduce polyp recruitment (e.g. Hoover 2005) should be conducted. Greater care should be taken to prevent transport of gelatinous species to different environments. Transport of pelagic stages (e.g. *Mnemiopsis leidyi*) and polyp stages is possible (e.g. *Cassiopea* spp., Bolton & Graham 2006). Many species may easily survive transport because the benthic stages enter a dormant stage (cyst or stolon) in response to stressful conditions in which they can survive extended periods (e.g. Arai 1997, Boero et al. 2002). Given the many trends of marine ecosystem modification, increases in jellyfish populations and blooms seem likely.

### Benefits of jellyfish to humans

Although the preceding discussion presents human problems with pelagic cnidarians and ctenophores, these organisms also provide ecological and commercial benefits for some human interests. Jellyfish may indirectly and directly benefit fish prey populations. Large jellyfish species often eat smaller species, which may be more voracious consumers (reviewed most recently in Arai 2005). In Chesapeake Bay, for example, *Chrysaora quinquecirrha* scyphomedusae can control the population of *Mnemiopsis leidyi* ctenophores thus reducing predation on bivalve veligers (Purcell et al. 1991) and on copepods (Purcell & Decker 2005). Juveniles of several commercially important species also associate with large jellyfish (>80 known species pairs; reviewed in Purcell & Arai 2001). The benefit for the fish has been assumed to be shelter and food, and recently positive correlations between juvenile whiting *Merlangius merlangus* survival and jellyfish abundance were shown in the North Sea (Lynam & Brierley 2006).

*Aurelia aurita* medusae and catches of associated butterfish dramatically increased in the 1990s, while other fish species declined in the Seto Inland Sea, Japan (Uye & Ueta 2004) where butterfish are harvested commercially.

Furthermore, although jellyfish often are considered to be 'dead-ends' in the food web, they provide food for many vertebrates including commercially important fishes, sea turtles, and humans (Hsieh et al. 2001, Omori & Nakano 2001, Purcell & Arai 2001, Arai 2005). The global production of jellyfish for human consumption has increased dramatically since the 1980s (Fig. 6) (FAO 2007). Most (99.9%) of the jellyfish fisheries are in Asia, although recently Australia (1997), the USA (1999), Europe, Africa (2000) and South America (2005) began small fisheries (FAO 2007). The economic value of jellyfish production in 2005 was estimated at US\$121 million (FAO 2007). In addition to commercial jellyfish fishing and processing, communities harvest jellyfish for local consumption. For example, aboriginal people in Taitung, Taiwan eat cubomedusae and scyphomedusae (J. E. Purcell & W. T. Lo pers. obs.). Jellyfish historically were believed to have health benefits (Hsieh et al. 2001), and recently clinical benefits are being demonstrated for arthritis and immunostimulation (Hsieh et al. 2001, Sugahara et al. 2006). Green fluorescent protein (GFP), which was originally isolated from the hydromedusan, *Aequorea victoria*, is known universally among molecular biologists and has led to a 'revolution in biotechnology' of inestimable value to humankind (Zimmer 2005). Finally, jellyfish are now exhibited in aquariums around the world providing recreational and educational benefits to millions of people annually. Perhaps the best human strategy for the future regarding jellyfish is to develop new jellyfish products for food and medicine (e.g. Webb 2007).

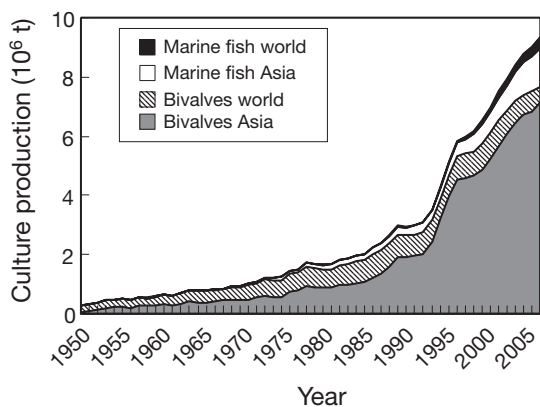


Fig. 5. Global and Asian bivalve and marine fish aquaculture production from 1950 to 2005 (FAO 2007)

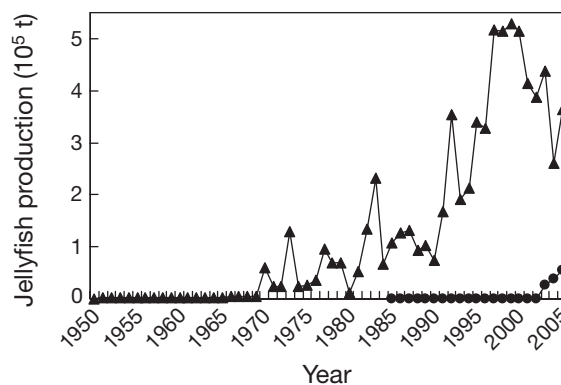


Fig. 6. Global jellyfish aquaculture (●) and total (▲) production from 1950 to 2005 (FAO 2007). Aquaculture production was zero before 2003

**Acknowledgements.** This research was partially supported by grants from the Japan Society for the Promotion of Science to S.U. (16405001) and the National Science Council and the Ministry of Education of the Republic of China to W.T.L. (NSC91-2621-Z 110-001, 94-C030220 [Kuroshio project]). We thank R. D. Brodeur and 3 anonymous reviewers for comments that improved this review. This paper is dedicated to the memory of Dr F. Pagés, a valued friend and colleague.

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*Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany*

*Submitted: January 18, 2007; Accepted: June 7, 2007  
Proofs received from author(s): October 24, 2007*