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Report of Working Group 26 on Jellyfish Blooms around the North Pacific Rim: Causes and Consequences

Edited by
Shin-ichi Uye and Richard D. Brodeur

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North Pacific Marine Science Organization (PICES)
P.O. Box 6000, Sidney, BC, V8L 4B2, Canada
E-mail: secretariat@pices.int
www.pices.int

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In Memoriam

Jennifer Purcell

Shannon Point Marine Center, Western Washington University, Anacortes, Washington, USA

Dr. Mary Needler Arai passed away on September 6, 2017, just one week shy of her 85th birthday. Mary dedicated her life to science and to her family. Raised in a family of matter-of-fact Canadian feminists and marine biologists long before feminism became mainstream, she shared a scientific pedigree that included significant major contributions to marine biology made by her grandmother and mother. Mary promoted women's participation in marine science both through her own scientific contributions and mentoring and more recently through her historical review of nearly a century of the contributions by women scientists to Canadian marine science. Throughout her entire career, Mary was a role model for women in science due to her exceptional scholarship, kindness, and integrity, as well as her intelligence and class.

Mary obtained a B.Sc. (Hons.) in Biology from the University of New Brunswick in 1952, an M.A. in Zoology from the University of Toronto in 1956 (working partly in Toronto and partly in England at University College London and the Plymouth Marine Biological Laboratory), and a Ph.D. at the University of California, Los Angeles (UCLA) in 1962.

At UCLA, Mary Needler married fellow graduate student, Hisao Arai, a parasitologist. Their long partnership connected their scientific interests in the North Pacific. Mary became one of the first of the few experts on parasites that include both jellyfish and fish in their life cycles, which are included in two of her review papers on the interactions of jellyfish and fish. Partly because those complex cycles rely on fish consuming jellies, Mary was also especially interested in fish as predators of jellies. Mary was employed for most of her professional career from Assistant to Full Professor (1969–1996) in the Department of Biology at the University of Calgary where Hisao was a tenured Professor. They spent every summer doing research at the family property adjacent to the Pacific Biological Station in Nanaimo, British Columbia. After their retirement in 1996, both Mary and Hisao continued their research full time after moving to Nanaimo. Their retirement home, which they designed, included a laboratory and an extensive scientific library. As a true scholar, Mary believed in knowing all scientific contributions on a subject and led to her writing numerous review papers that reflected her encyclopedic knowledge.

The jellyfish community benefited greatly from Mary's scientific work. Some of the papers she published on jellyfish focused on topics that the wider research community realized the importance of only decades later. Some studies remain unique to this day, such as her works on prey chemically stimulating jellyfish to feed and on digestion of jellyfish by fish. In 1997, Mary published an exceptionally important book on "*A Functional Biology of Scyphozoa*" that continues to be a unique and valuable resource. Her contributions to knowledge about jellyfish were honored in 2013 with a Lifetime Achievement Award at The International Jellyfish Bloom Symposium in Hiroshima, Japan.

Mary contributed to knowledge on jellyfish and their connections to fish through much of her academic career. She contributed to PICES Annual Meetings beginning in 2000 in Hakodate, Japan (Arai *et al*., *Predation by fish, especially chum salmon, on North Pacific coelenterates*). She was an important contributor to PICES Working Group 26 which was established in 2010 and this PICES Scientific Report No. 51 (*Report of Working Group 26 on Jellyfish Blooms around the North Pacific Rim: Causes and Consequences*). She attended two meetings of the Working Group in Hiroshima, Japan, in 2012 as part of the Fourth International Jellyfish Blooms Symposium where she received the Lifetime Achievement Award, and in 2013 as the last informal Working Group meeting held in Nanaimo in 2013.

The scientific community was lucky to have Mary and to benefit from her many contributions. Mary, in turn, was blessed by true passion for her chosen area of study and to be able to contribute to those interests throughout her long and productive life. Her scientific legacy and influence will live on for many years. She will be sorely missed by her many friends and colleagues in the PICES community.

Dr. Mary Needler Arai

Executive Summary

The Working Group on *Jellyfish Blooms around the North Pacific Rim: Causes and Consequences* (WG 26) was established in October 2010 at PICES-2010 in Portland, Oregon, USA, in the face of growing recognition of a global increase in jellyfish populations. The objectives of the WG were to: 1) review past and ongoing studies on bloom-forming jellyfish being conducted somewhat independently (or nationally) in each PICES member country in order to assess the general trend of jellyfish populations in the North Pacific and its marginal seas, 2) identify causes for recurrent jellyfish blooms, and 3) understand their ecological and socio-economic impacts. The final goal was to forecast future jellyfish population trends and associated impacts in the PICES region and to provide recommendations for reducing their negative impacts. To achieve this goal, the WG adopted the following terms of reference:

1. Review past and ongoing studies on the reproductive biology of jellyfish species that cause problematic blooms;
2. Compile existing data on temporal variations in jellyfish abundance in the North Pacific and its marginal seas, and analyze them in relation to regional environmental and climate changes in order to identify causes of increasingly recurrent jellyfish blooms;
3. Elucidate the role of jellyfish in coastal and oceanic marine food webs and assess the impacts of jellyfish blooms on marine ecosystems and socio-economies such as fisheries and aquaculture;
4. Evaluate methodologies for predicting blooms and for diminishing their impact on marine and human systems, including bloom forecast modeling and the modification of fishing gears;
5. Promote international collaboration among PICES member countries for exchanging available information on jellyfish, and encourage joint research surveys on jellyfish among PICES member countries;
6. Provide jellyfish metrics as an indicator of ecosystem change and resiliency in cooperation with FUTURE AICE-AP and SOFE-AP and FUTURE related expert groups;
7. Publish a final report summarizing the results, including recommendations to policy makers for reducing impacts of jellyfish blooms in the North Pacific.

The life history and population dynamics of jellyfish, which commonly refer to gelatinous zooplankton belonging to three phyla: Cnidaria (classes Hydrozoa, Scyphozoa, and Cubozoa), Ctenophora, and Chordata (class Thaliacea), have been reviewed. For four representative bloom-forming scyphozoans, *i.e.*, *Aurelia aurita* s.l., *Chrysaora pacifica*, *Cyanea nozakii*, and *Nemopilema nomurai*, the species-specific life cycle and reproductive patterns have been described, emphasizing that asexual reproduction by the polyp stage is the key to determining the magnitude of medusa population size.

For robust assessment of jellyfish spatio-temporal distribution and abundance, orthodox methods by means of plankton and/or trawl nets are often insufficient, due to their body fragility, patchy distribution, and clear seasonality. Hence, concurrent use of acoustic instruments (*e.g.*, multi-frequency echosounders and Dual-Frequency Indentification Sonar) and underwater video cameras, in addition to aerial and ship sightings, is recommended.

The spatio-temporal variations of biomass and bloom conditions of jellyfish have been reviewed for the following 10 regions in the North Pacific and its marginal seas: 1) west coast of the United States, 2) west coast of Canada, 3) Salish Sea, 4) Gulf of Alaska, 5) Bering Sea, 6) Okhotsk Sea, 7) Western North Pacific Ocean, 8) Japanese coast, 9) Korean coast, and 10) Chinese coast. Jellyfish taxonomic composition and year-to-year occurrence patterns differ greatly from one region to another, depending primarily on regional differences in natural environmental and climate changes (*e.g.*, regime shifts) in addition to anthropogenic impacts (*e.g.*, eutrophication, marine construction, and over-fishing). In Chinese, Japanese and Korean coastal waters, where anthropogenic impacts are much more pronounced than in the other PICES regions, jellyfish blooms have become increasingly frequent and more extent in recent decades so as to cause severe damage to fisheries, power plant operations and tourism. So far, accumulated scientific evidence is still insufficient to identify which factors are responsible for the rise of jellyfish populations.

Cnidarian jellyfish are carnivores, eating almost any available zooplankton taxa (*e.g.*, copepods, euphausiids, benthos larvae, fish eggs and larvae, and other gelatinous zooplankton) and constitute competitors with, as well as predators on, planktivorous fish. Jellyfish are preyed upon by many predators, including fishes, sea turtles, sea birds, and other gelatinous predators.

Jellyfish and their ecosystems provide a variety benefits to humankind, or ecosystem services, among which the direct utilization of jellyfish, primarily rhizostomes, as human food is the most beneficial aspect. When jellyfish populations produce massive blooms, their adverse impacts on intrinsic ecosystem services of the ocean become more conspicuous, as manifested by increased damage in fisheries, aquaculture, power plant operations, and tourism.

This report concludes with recommendations to policy makers and suggestions for future research to mitigate the effects of jellyfish blooms. To reduce jellyfish negative impacts, it is necessary to establish routine monitoring programs. Based on accumulated data in both Korean and Japanese jellyfish monitoring programs, which started in 2005 and 2006, respectively, it is possible to forecast *N. nomurai* bloom intensity in June or July of each year, 1–3 months prior to the peak bloom season. Thus, Korean and Japanese fishermen can take proper countermeasures in advance of the blooms, such as modification of fishing nets (*i.e.*, installation of jellyfish excluding devices). Physical elimination with high-pressure water jets of polyps attached to artificial substrates, and intensive slicing of locally aggregated medusae may also be effective as countermeasures.

1 Introduction

Richard Brodeur[1] and Shin-ichi Uye[2]

[1] Northwest Fisheries Science Center, Hatfield Marine Science Center, National Marine Fisheries Service, Newport, Oregon, USA
[2] Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Japan

1.1 Background and Formation of the Working Group

Similar to many other regions in the world, the North Pacific Ocean and its surrounding marginal seas have experienced high numbers of jellyfish in recent years, culminating in massive blooms in some coastal areas. The North Pacific is among the most productive regions in the world in terms of fisheries catch, and supports the livelihood of millions of fishermen, and hence millions of people, especially those living in Asia who are highly dependent on the ocean for their nutritional needs. Scientists and managers have become increasingly concerned about the rise in the prevalence and magnitude of these blooms in recent years and their potential impact on ecosystem services such as fisheries, tourism, and power generation. The North Pacific Marine Science Organization (PICES) has long recognized the importance of gelatinous zooplankton in the ecosystem and the present limitations to our understanding of what initiates and maintains the blooms and their effects on other marine resources.

The establishment of a working group on jellyfish was suggested as early as 2007, but it was at PICES-2009 in Jeju, Korea, that the idea took off and was extensively, but informally, discussed by several PICES scientists interested in forming such a group. The Biological Oceanography Committee strongly supported the initiative, and at PICES-2010 in Portland, USA, a new PICES Working Group on *Jellyfish Blooms around the North Pacific Rim: Causes and Consequence* (WG 26) was established with the explicit goal of bringing experts together from the member countries to address this issue and to come up with potential solutions to reverse the increasing trend in jellyfish blooms in coastal waters. The terms of reference and scientists from each country who made up the group can be found in Appendices 1 and 2.

1.2 Working Group Timeline

The WG met for the first time at PICES-2011 in Khabarovsk, Russia. Fourteen out of 20 WG members attended this inaugural meeting. In order to grasp the general status of the jellyfish blooms around the North Pacific Rim, information about current and past jellyfish blooms and related research was presented for each member country.

- Lucas Brotz (University of British Columbia) presented a summary for Canada and found that jellyfish abundance has fluctuated over the recent decades but did not show any significant increases in Canadian Pacific coastal waters. He then reported on trends in global jellyfish blooms, based on various sources of information from scientific literature to mass media articles. His results suggest that jellyfish have increased globally in recent decades, with some certainty, in the majority (~70%) of 64 Large Marine Ecosystems of the world, and these increases seem to be related to human impacts.

- China currently runs two big national projects on jellyfish blooms. Siqing Chen (Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences) described the project entitled "Key Process, Mechanism and Ecological Consequences of Jellyfish Blooms in Chinese Coastal Waters" which aims to understand the causes of jellyfish blooms in Chinese waters and their impacts on the ecosystem. Zijun Xu (North China Sea Environmental Monitoring Center, State Oceanic Administration) explained the other project which focuses mainly on the establishment of a monitoring system for early warning of possible jellyfish blooms and determining techniques for minimizing their impacts on human society.

- Japanese waters are substantially affected by jellyfish blooms, most intensively by the moon jellyfish *Aurelia aurita* s.l. and the giant jellyfish *Nemopilema nomurai*. Japanese scientists are examining the jellyfish problems under two major projects. Hideki Akiyama (Seikai National Fisheries Research Institute, Fisheries Research Agency) reported on the China-Japan-Korea International Project on the Giant Jellyfish Bloom which includes a monitoring component and development of predictive indices. Shin-ichi Uye (Hiroshima University) summarized the results from the Studies on Prediction and Control of Jellyfish Outbreak (STOPJELLY) project which aims to understand factors leading to the blooms, predict their severity, and develop chemical and biological methods to control jellyfish populations.

- Changhoon Han (National Fisheries Research and Development Institute, Ministry of Oceans and Fisheries) explained that Korea is also suffering from jellyfish blooms, with a total economic loss of 265 million USD in an intense bloom year. The Korean government has established a Jellyfish Monitoring and Countermeasure Center to tackle this problem and has initiated a program to minimize jellyfish damage to fisheries and tourism.

- Alexander Zavolokin (Pacific Scientific Research and Fisheries Center, TINRO-Center) reported that Russian scientists have been studying jellyfish (mainly taxonomic composition, abundance and biomass) since 1990 in the western Bering Sea, Okhotsk Sea and other Russian waters by trawl netting, sampling more than 10,000 stations in these regions. According to the results of these studies, the annual jellyfish biomass has fluctuated widely but did not show any consistent trends in the Bering Sea or Okhotsk Sea.

- Jennifer Purcell (Shannon Point Marine Center, Western Washington University) spoke on the jellyfish biomass in the eastern Bering Sea where jellyfish data have been consistently monitored since 1979. Biomass increased in the 1990s and declined substantially for 8 years after 2000, but has been increasing since 2009. She also presented the geographical distribution of jellyfish along Puget Sound, Washington State, where they are more abundant in waters adjacent to more populated cities, indicating some of the effects by human activity on jellyfish population increase. Finally, studies along the U.S. west coast were summarized, which have attempted to link jellyfish biomass with environmental changes.

At PICES-2012 (Hiroshima, Japan), WG 26 held a very successful BIO/FIS Topic Session on "*Jellyfish in marine ecosystems and their interactions with fish and fisheries*" that was co-sponsored by ICES which also had strong interest in the impact of jellyfish in fisheries. The session was highly popular, with 18 oral presentations and 11 posters dedicated to the topic (see Appendix 3 for a summary of the topic session). The WG meeting included discussions on final report content and how it might best address the goals and themes of PICES' FUTURE program, as well as a request for PICES co-sponsorship of the Fourth International Jellyfish Bloom Symposium to be held in Hiroshima in 2013. This request was subsequently endorsed by Science Board and approved by Governing Council. During the Annual Meeting many of the WG members were able to meet informally with a group of scientists planning to construct ecosystem models for many regions heavily impacted by jellyfish. The project plans were to put together holistic ecosystem models for the PICES region as well as two non-PICES regions (Gulf of Mexico and Humboldt Current) in the coming years and examine the impact jellyfish have on trophic structure, particularly related to their effect on forage fishes. This work will likely contribute useful information to the management of these ecosystems in the future.

WG 26's third meeting was held inter-sessionally in Hiroshima prior to the Fourth International Jellyfish Blooms Symposium (June 5–7, 2013; see PICES Press, Vol. 21, No. 2 in Appendix 4 for a report on the Symposium). All PICES member countries were represented at this meeting and several prominent jellyfish scientists from non-PICES countries also attended and provided useful comments and suggestions.

WG 26 did not have an official meeting at PICES-2013 (Nanaimo, Canada). Co-Chair, Dr. Richard Brodeur, who was planning to convene the meeting was unable to attend due to unexpected U.S. travel restrictions imposed on government employees. However, several WG members who were in attendance did meet informally. A proposal for an ICES/PICES Theme Session on "*Gelatinous zooplankton on a global perspective: interactions with fisheries and consequences for socio-economics*" at the ICES 2014 Annual Science Conference in A Coruña, Spain was endorsed by Science Board and approved by Governing Council. This was a follow-up to the very successful PICES/ICES collaborative session held at PICES-2012. In contrast to the earlier session, this one focused on the socio-economic impacts of blooms on humans, particularly related to fisheries. Dr. Brodeur was a PICES co-convenor, and Dr. Shin-ichi Uye was an invited speaker. Attesting to the high caliber of presentations at the theme session, both ICES awards for best presentations by an early career scientist went to the presenters in this session (see Appendix 3 for a summary of the session and award recipients).

The following is a summary of WG 26's activities, accomplishments, and recommendations.

2 Life History and Population Dynamics

Jennifer Purcell[1] and Shin-ichi Uye[2]

[1] Shannon Point Marine Center, Western Washington University, Anacortes, Washington, USA
[2] Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Japan

2.1 Introduction

The term jellyfish is most often used to describe the free-swimming (medusoid) stage of the phylum Cnidaria (classes Hydrozoa, Scyphozoa, and Cubozoa), although it has been used to include the phylum Ctenophora (comb jellyfish without stinging cells) and the phylum Chordata (class Thaliacea, pelagic tunicates without stinging cells). In addition to the fact that they sting, jellyfish are known for their rapid population growth. Most species have seasonal peaks in abundance, usually in spring through summer that coincides with local patterns of plankton production. Most types of jellyfish in the phylum Cnidaria have a life cycle that includes an asexually reproducing stage attached to hard surfaces ("polyp") in addition to the swimming sexual medusa stage (Table 2.1.1).

Table 2.1.1 Summary of jellyfish (Cnidaria, Ctenophora and Chordata) life cycles.

Taxon	Number/ Representative species	Benthic stages	Pelagic stages	References
CNIDARIA				
Hydromedusae	>800	hydroid	planula, medusa	Arai and Brinkmann-Voss, 1980; Bouillon *et al*., 1993
Anthomedusae	*Sarsia tubulosa*	yes	yes	Arai and Brinkmann-Voss, 1980; Bouillon *et al*., 1993
Leptomedusae	*Aequorea* spp.	yes	yes	Arai and Brinkmann-Voss, 1980; Bouillon *et al*., 1993
Limnomedusae	*Proboscidactyla fiavicirraa*	yes	yes	Arai and Brinkmann-Voss, 1980; Bouillon *et al*., 1993
Trachymedusae	*Aglantha digitale*	no	yes	Arai and Fulton, 1973; Arai and Brinkmann-Voss, 1980; Bouillon *et al*., 1993
Narcomedusae	*Solmaris corona*	no	yes	Arai and Brinkmann-Voss, 1980; Bouillon *et al*., 1993
Siphomedusae	>250	no	eudoxid, polygastric	Bouillon *et al*., 1993

Table 2.1.1 Continued.

Taxon	Number/ Representative species	Benthic stages	Pelagic stages	References
CNIDARIA				
Scyphomedusae	> 200	Scyphistoma (polyp), podocyst	planula, ephyra, medusa	Arai, 1997
Semeostomae	*Aurelia* spp.	yes (all species but *P. noctiluca*)	yes	Arai, 1997; Straehler-Pohl and Jarms, 2010; Straehler-Pohl *et al*., 2011; Holst, 2012
	Pelagia noctiluca	no	yes	
Rhizostomae	*Nemopilema nomuri*	yes (all species)	yes	Ding and Chen, 1981; Kawahara *et al*., 2006; Schiariti *et al*., 2008; Straehler-Pohl and Jarms, 2010; Fuentes *et al*., 2011
Coronatae	*Linuche unguiculata*	colonial scyphistoma (all species but *P. periphylla*)	yes	Jarms, 2010; Jarms *et al*., 2002; Straehler-Pohl and Jarms, 2010
	Periphylla periphylla	no	yes	
Cubomedusae	*Carybdea* spp.	cubopolyp	medusa	Werner *et al*., 1971
CTENOPHORA	*Bolinopsis* spp.	no	cydippid larva, ctenophore	Wrobel and Mills, 1998
CHORDATA	*Thalia democratica*	no	yes	Heron, 1972

2.2 Phylum Cnidaria – Class Hydrozoa

Hydromedusae form a diverse group (>800 species worldwide), most of which are <1 cm in size and transparent, thereby going mostly unnoticed by humans. The small medusae can be collected with standard net and preservation techniques. Many species in the orders Anthomedusae, Leptomedusae, and Limnomedusae produce tiny jellyfish asexually from the colonial hydroid stage, which live attached to hard surfaces including docks and aquaculture rafts, and are defined as meroplanktonic (Fig. 2.2.1A, B). The orders Trachymedusae and Narcomedusae are holoplanktonic, *i.e.*, lacking an attached, benthic stage (Fig. 2.2.1C).

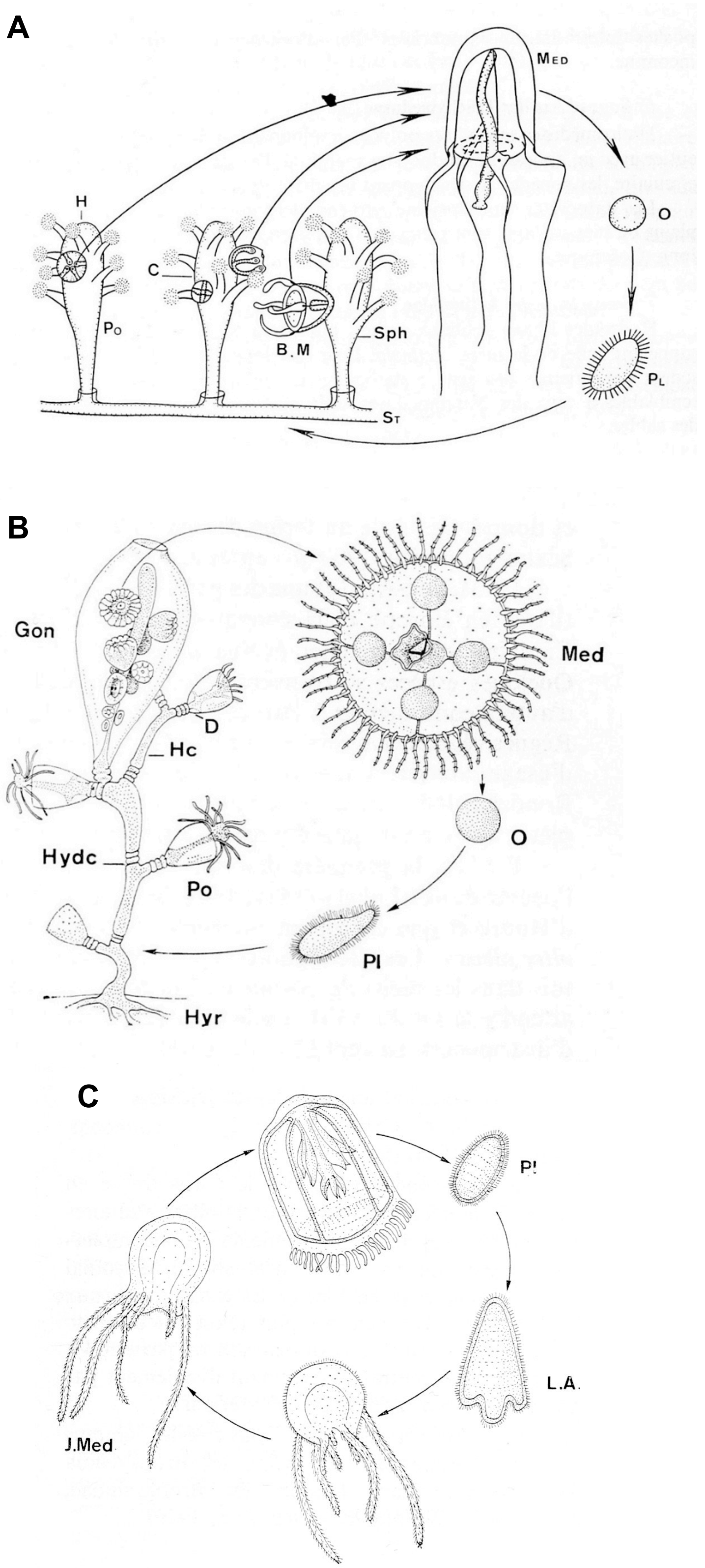

Fig. 2.2.1 Hydromedusa life cycles. (A) meroplanktonic Anthomedusae, (B) meroplanktonic Leptomedusae, (C) holoplanktonic Trachymedusae (from Bouillon *et al*., 1993).

Siphonophores (Order Siphonophorae) comprise over 250 species of colonial, holoplanktonic cnidarians that range in size from centimeters to several meters in length. The commonly recognized species, *Velella velella*, is the only one that floats at the surface. The other species occur throughout the water column to the bottom and are often the most numerous gelatinous species collected by standard methods. However, their colonies break into pieces. Two suborders (Physonectae and Cystonectae) have sexually reproductive members that remain attached to the colony. In the third suborder (Calycophorae), species such as *Muggiaea atlantica* produce many free sexual stages (eudoxids) that are generally <1 cm in size (Fig. 2.2.2).

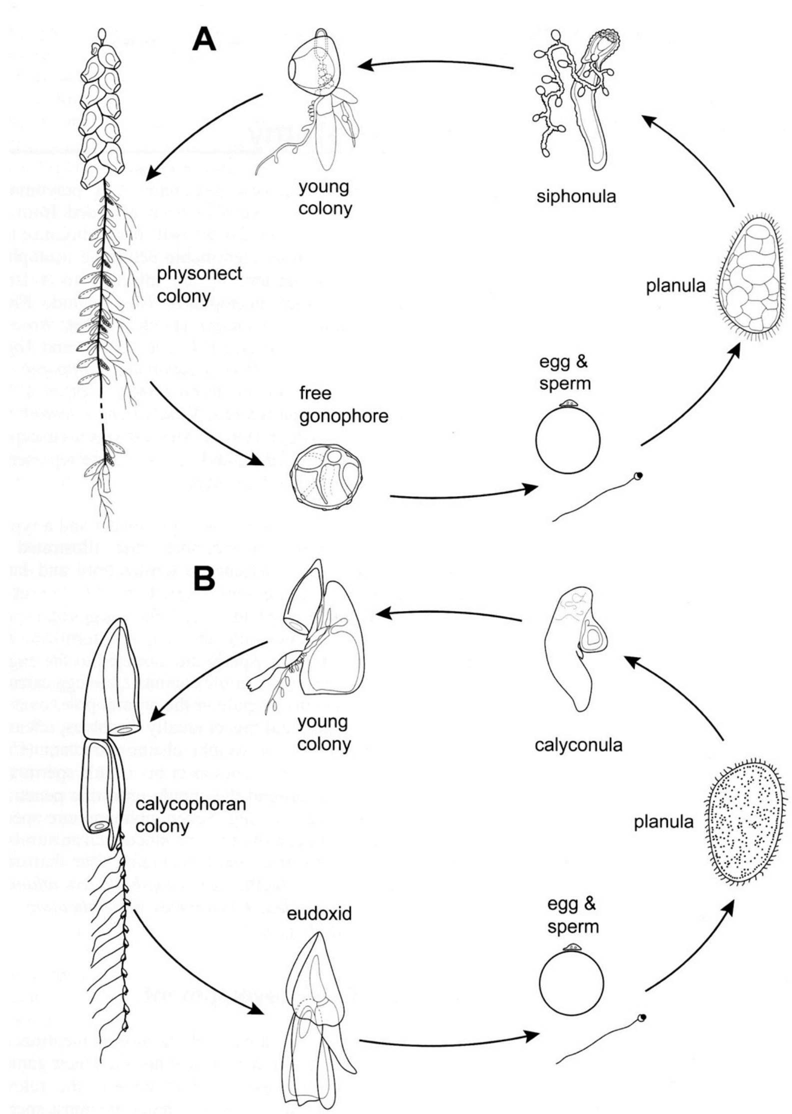

Fig. 2.2.2 Siphonophore holoplanktonic life cycles. (A) Physonectae, (B) Calycophorae (from Bouillon *et al*., 1993).

2.3 Phylum Cnidaria – Class Scyphozoa

Semeaostome, rhizostome, and coronate scyphomedusae are generally large jellyfish that have a polyp stage attached to hard surfaces, which asexually produces more polyps by budding or creating small cysts (podocysts) (Fig. 2.3.1A). Polyps also strobilate (undergo a form of transverse fission) to asexually produce one to several new medusae (ephyrae: 1–2 mm in diameter), which then mature into sexually reproductive medusae. In temperate waters, strobilation usually occurs during the seasonal transition to spring. Fertilization can occur in the water, or within the female medusae, which then brood the larvae (planulae).

Some scyphozoans are holoplanktonic. *Pelagia noctiluca* is the only semeaostome known to lack an asexual benthic stage but develops from fertilized eggs in the water column (Rottini Sandrini and Avian, 1983; Fig. 2.3.1B). *Periphylla periphylla*, however, lacks benthic as well as the planula and ephyra stages (Jarms *et al*., 1999). Although three of seven families in the order Coronatae are exclusively deep-sea species, some of their colonial polyps have been recovered from stony corals dredged from depths of only 133–808 m (Jarms *et al*., 2002; Fig. 2.3.1).

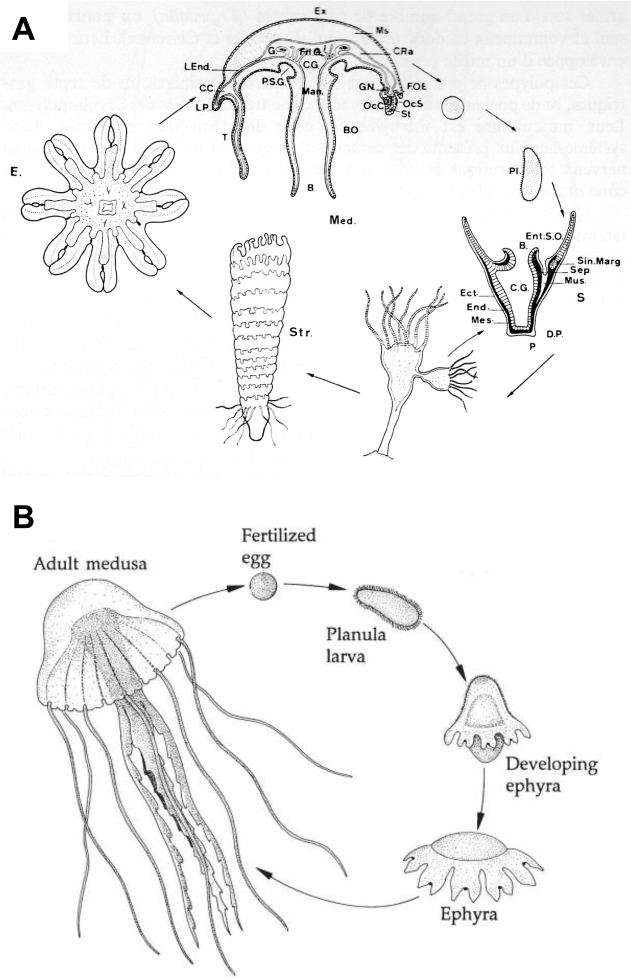

Fig. 2.3.1 Scyphozoan life cycles. (A) simplified meroplanktonic scyphozoan (from Bouillon *et al*., 1993), (B) holoplanktonic *Pelagia noctiluca* (from Brusca and Brusca, 2003).

2.3.1 Seasonal life cycle of Scyphozoa

Semeaostomes

Scyphozoan jellyfishes, such as *Chrysaora pacifica*, *Cyanea nozakii* and *Aurelia aurita* s.l. (*Aurelia* sp. 1)[1], have a typical life cycle alternating between a sexual medusa phase and an asexual polyp phase. In the Inland Sea of Japan, the occurrence of their medusae is generally confined to the periods between March and August for *C. pacifica* (Ueda, 2007; Uye, pers. observation), between April and September for *A. aurita* s.l. (Uye and Shimauchi, 2005) and between May and December for *C. nozakii* (Kinoshita *et al*., 2000; Uye, pers. observation). Prior to their occurrence, ephyrae, the earliest planktonic stage, are released from benthic polyps, which reproduce asexually. A common mode of asexual reproduction by semaeostome polyps is podocyst formation. Podocysts consist of a mass of cells having rich nutrient reserves and few organelles, and are enclosed by a robust chitinous capsule to avoid predation by the natural enemies of polyps, such as nudibranchs, and to prevent infestation by bacteria and fungi (Chapman, 1968; Blanquet, 1972; Black, 1981; Ikeda *et al*., 2011a). These characteristics enable podocysts to remain dormant for 3.2 years in *A. aurita* s.l. and at least a year in *C. pacifica* and *C. nozakii* (Thein *et al*., 2012, 2013). After dormancy, they are capable of excysting into active polyps, which continue asexual reproduction. Podocyst formation is the only method of asexual reproduction in *C. pacifica* and *C. nozakii* (Kakinuma, 1967; Dong *et al*., 2008), and its production rate accelerates with the increase in temperature and food supply (Thein *et al*., 2013). In *A. aurita* s.l. polyps, however, direct budding is the primary reproductive mode, and podocysts are formed by its polyps only when they are starved (Han and Uye, 2010; Thein *et al*., 2012). In these three species, the excystment of dormant podocysts is induced by exposure to low temperatures and hypoxia (Thein *et al*., 2012, 2013).

The seasonal life cycles of *C. pacifica*, *C. nozakii*, and *A. aurita* s.l. in the Inland Sea of Japan are schematically depicted in Fig. 2.3.2 (Thein *et al*., 2013). The seasonal patterns in podocyst production and excystment are basically similar among these species: their podocysts are produced mainly in summer and excyst mostly in autumn to increase their polyp populations. Furthermore, in *A. aurita* s.l., the polyps reproduce by budding during summer to autumn, attaining much higher production rates than the other two species. Strobilation is induced at temperatures ≤18°C for *C. pacifica* polyps (Thein *et al*., 2013) and at temperatures ≤15°C for *A. aurita* s.l. polyps (Han and Uye, 2010; Thein *et al*., 2012), indicating that winter is the main season for their strobilation and ephyra release. The strobilation of *C. nozakii* takes place after that of *C. pacifica* and *A. aurita* s.l., mainly in late spring when the seasonal occurrence of its medusa follows that of the other two species. The time sequence of podocyst excystment and strobilation suggests that the polyps newly emerged from podocysts in autumn contribute to the production of ephyrae in the subsequent season in all three species.

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[1] Now referred to as *Aurelia* sp. 1 from DNA sequence analysis (Dawson and Jacobs, 2001; Endo *et al*., 2011). Both versions will be given elsewhere in the report.

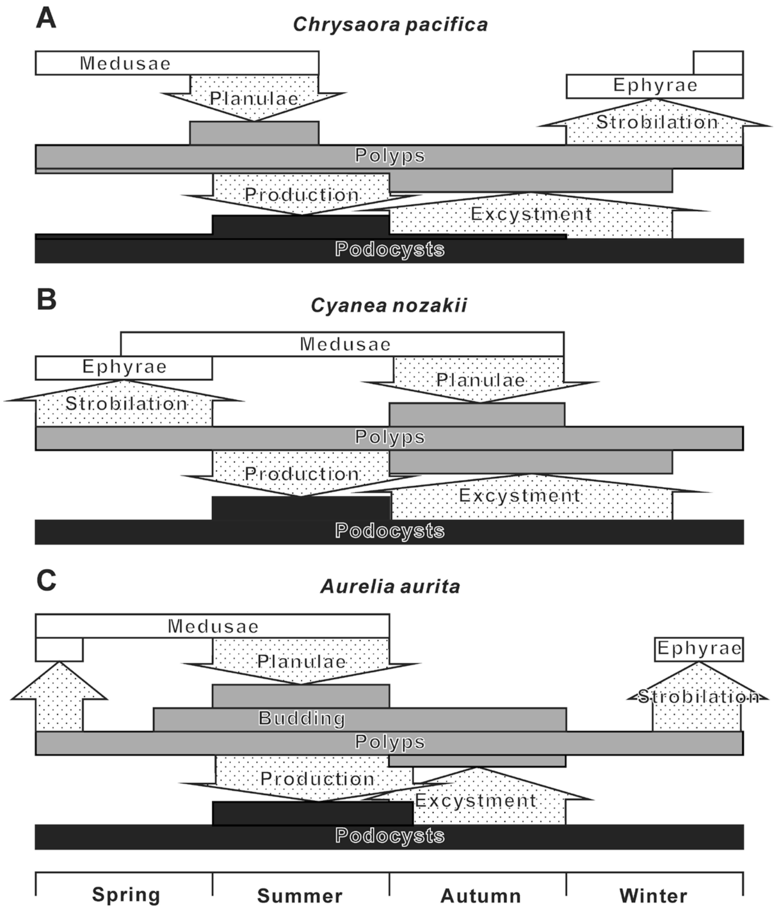


Fig. 2.3.2 Schematic diagram of the seasonal life cycles of (A) *Chrysaora pacifica*, (B) *Cyanea nozakii*, and (C) *Aurelia aurita* s.l., with special emphasis on the behavior of polyps and podocysts. Arrows indicate the direction of propagation (from Thein *et al*., 2013).

Rhizostomes

The rhizostome *Nemopilema nomurai* is a gonochoristic jellyfish having conspicuous genital organs protruding as large sacs beneath its bell. The genital organ is folded into many layers like a gathered drape, so that the ribbon-like testis or ovary located at the bottom of the bell can increase in length and surface area (Fig. 2.3.3, Ohtsu *et al*., 2007). A schematic drawing of a cross-sectional view of the ovary of (Fig. 2.3.4) demonstrates that the genital wall consists of three layers: a gastrovascular epithelium of endodermal origin, a genital outer epithelium of ectodermal origin and a mesogleal tissue between the two epithelia. The ovary consists of two gastrodermal tissue sheets with mesoglea sandwiched between these sheets, and its proximal end merges with the genital wall through an interlinking thin process. Along the basal part of the ovary, a small invaginated area, or a gastric-filament groove, is observed, inside of which innumerable gastric filaments are concentrated. The ovary extends undulating, peripherally close to the genital wall. There is a narrow space, or subgenital sinus, between the ovary and the genital wall, occupied by a highly viscous mucus-like substance. The subgenital sinus connects to the gastrovascular cavity through a peripheral opening. In males, the morphological structures of the testis are basically similar to those of the ovary, except that the testis contains sperm follicles instead of oocytes (Ohtsu *et al*., 2007).

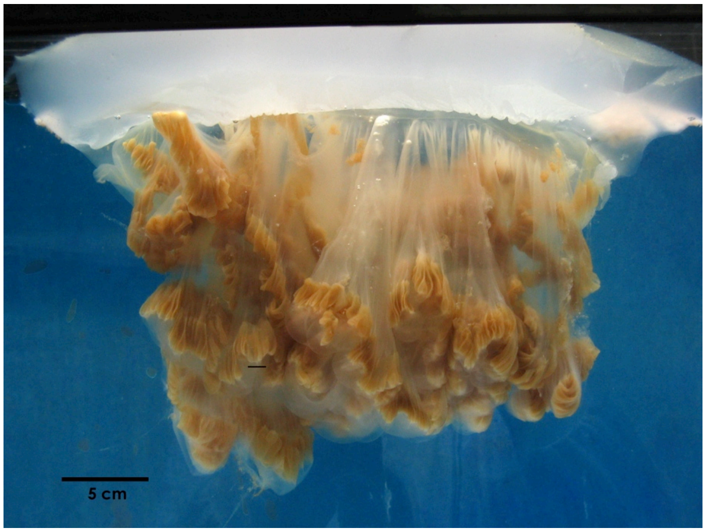


Fig. 2.3.3 View of a *Nemopilema nomurai* ovary contained in the gastric pouch protruding beneath the bell. The gastric pouch is a large sac with numerous folds like drapes. The ovarian tissue is located at the bottom of each fold (from Ohtsu *et al*., 2007).

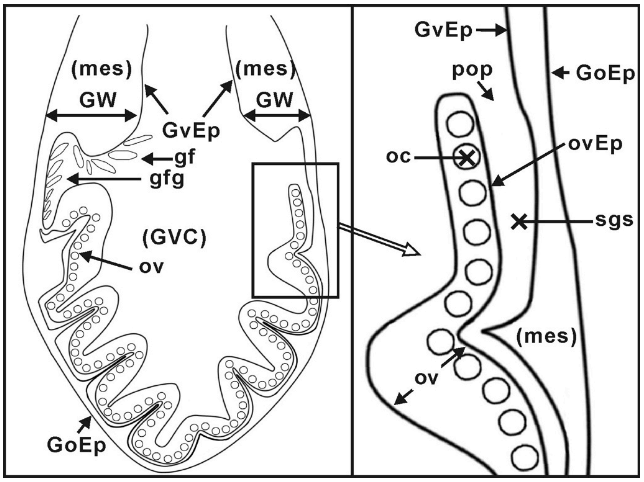


Fig. 2.3.4 A schematic drawing of a cross-sectional view of the female gonad of Nemopilema nomurai. gf: gastric filament, gfg: gastric filament groove, GoEp: genital outer epithelium, GVC: gastrovascular cavity, GvEp: gastrovascular epithelium, GW: genital wall, mes: mesoglea, oc: an oocyte, ov: ovary, ovEp: ovarian epithelium, pop: peripheral opening, sgs: subgenital sinus (from Ohtsu *et al.*, 2007).

Fecundity of two *N. nomurai* females with body masses of 20 and 56 kg were found to carry 160 million and 361 million oocytes, respectively (Uye *et al*., unpublished data). Assuming a positive relationship between fecundity and body size, the fecundity of the largest *N. nomurai* medusa (~200 kg) can attain more than one billion oocytes, greater than the fecundity of the ocean sunfish, *Mola mola* (~300 million for a female of 137 cm body length), famously the most fecund of all vertebrates (Schmidt, 1921; Carwardine, 1995). The enormous fecundity characteristic of this species may be a mechanism to produce population outbreaks when conditions are favorable. It may also be a biological adaptation to compensate for extremely high mortality of the population, or low recruitment to the medusa stage, in nature.

The translucent gonads gain color, varying from milky white through to pink and dark brown, mainly in November and December, indicating that late fall and early winter is the spawning season (Kawahara *et al*., 2006; Ohtsu *et al*., 2007; Iguchi *et al*., 2010). Even during the main spawning season there is large individual variation in the maturation stage. It is a peculiarity that physically intact and vigorously swimming medusae have exclusively immature gonads, and their gonadal maturation is induced only when the medusae are fatally damaged (Ohtsu *et al*., 2007; Ikeda *et al*., 2011b).

As depicted in Fig. 2.3.5, a primary oocyte arises from the ovarian epithelium of endodermal origin, protruding into the ovarian mesoglea. Ikeda *et al*. (2011b) has divided the oocyte maturation into five stages, from Stage 1 to Stage 5, with oocyte mean diameter of 35, 55, 78, 93 and 106 µm, respectively. The oocyte in Stage 1 and Stage 2 is in intimate contact with special epithelical cells called trophocytes which have microvilli located on the side of the subgenital sinus, and nutrients are transported from the subgenital sinus to the oocyte to form yolk bodies in the ooplasm adjacent to the trophocytes. Accumulation of nutrients also leads to the increase of yolk bodies near the Golgi complexes. The Stage 3 oocyte begins to separate from the trophocytes, and the Stage 4 oocyte is completely dissociated from them but bears developed microvilli over its surface through which nutrients from the surrounding mesoglea are taken up. Stage 5 is a mature oocyte which is filled with numerous yolk bodies in the cytoplasm with an extraordinarily large nucleus, indicating that the maturation division has stopped at the prophase of the first meiosis.

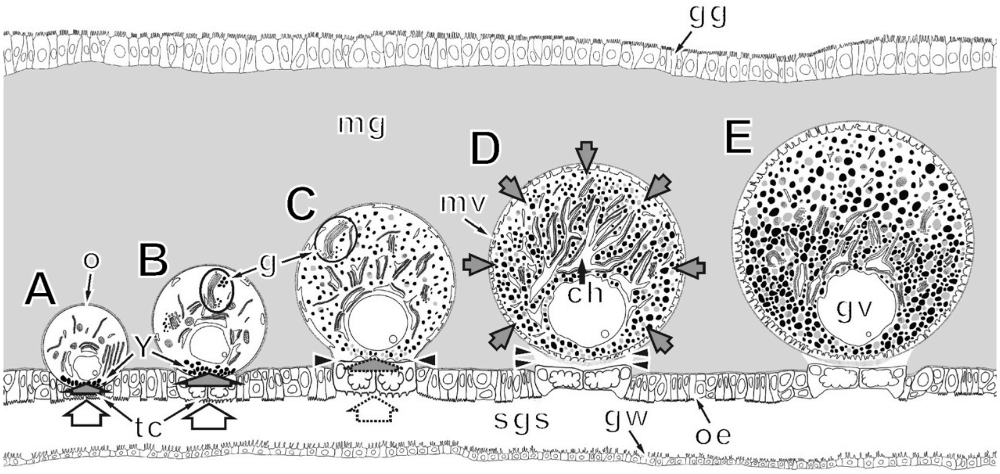


Fig. 2.3.5 Schematic diagram of the source of nutrients at various oocyte maturation stages of *Nemopilema nomurai*. (A) First stage. Trophocytes take nutrients from the subgenital sinus and transfer to the oocyte, which forms yolk bodies in the ooplasm adjacent to the trophocytes. (B) Second stage. Yolk deposition takes place in the oocyte adjacent to the trophocytes and near the Golgi complexes. (C) Third stage. The oocyte begins to separate from the trophocytes (arrowheads), and the transfer of nutrients by the trophocytes gradually decreases (broken-line arrows). (D) Fourth stage. The oocyte completely dissociates from the trophocytes (double arrowheads), but takes nutrients from the surrounding mesoglea through the developed microvilli located over the surface of the oocyte (thick grey arrows). Intraooplasmic channels form the wide networks (black arrow) in the ooplasm. (E) Fifth stage. ch: intraooplasmic channel, g: Golgi complex, gg: gonadal gastrodermis, gv: germinal vesicle, gw: genital wall, mg: mesoglea, mv: microvilli, o: an oocyte, oe: ovarian epithelium, sgs: subgenital sinus, tc: trophocytes, Y: yolk bodies (from Ikeda *et al*., 2011b).

In male *N. nomurai*, a primary sperm follicle arises from the testicular epithelium, protruding into the testicular mesoglea (Ikeda *et al*., 2011b). The sperm follicle keeps in contact with the trophocytes through which nutrients needed for spermatogenesis are transported from the subgenital sinus. As the maturation proceeds, the sperm follicle becomes larger and transforms in shape from a sphere (<50 µm diameter) to an ellipsoid (short and long diameter: ~70 and 120 µm, respectively) filled with spermatozoa. During spermatogenesis, a spermatocyte arising from the wall of the follicle undergoes meiosis two times to form four spermatozoa, each possessing a long conical head and a flagellum.

In artificially damaged medusae, maturation is completed within 3 days for females and 3–5 days for males to ready to spawn. In most wild medusae, however, gonadal maturation may progress more slowly, as the body is injured gradually by predation of jellyfish-eating fish and/or parasites, such the jellyfish shrimp *Latreutes anoplonyx* (Arai, 2005; Ohtsuka *et al*., 2009; Miyajima *et al*., 2011).

Light is an important factor to induce spawning in *N. nomurai* (Ohtsu *et al*., 2007; Ikeda *et al*., 2011b). The Stage 5 oocyte with a conspicuously large nucleus, whose maturation division stops at the prophase of the first meiosis, reinitiates the divisions by the breakdown of the germinal vesicle, about 1 hour after the light exposure. A 0.5 hour later, the trophocytes produce a gap to form an ovulation pit through which the oocyte passes out into the subgenital sinus. Spawned eggs are transported peripherally and are finally shed into the gastrovascular cavity. Daily spawning in response to light occurs for up to 4 days until all oocytes are released. Male spawning, or spermiation, is also induced by light exposure. Between 5 and 20 minutes after light exposure, the trophocytes dissociate each other to form a spermiation pit, and spermatozoa in the follicle are shed through the pit into the subgenital sinus. Spermiation lasts usually for 15 minutes, and daily spermiation is repeated for up to 6 successive days.

Judging from the importance of light, dawn may function as a light trigger for spawning of both eggs and sperm in wild *N. nomurai* (Fig. 2.3.6). Gametes are shed into the gastrovascular cavity and then released from the body through small orifices on the scapulets and oral arms. Fertilization may take place not only in the females' gastrovascular cavity into which sperm are drawn in from the surrounding water but also in the ambient water, suggesting that the proximity of mature females to males is important to ensure high rates of fertilization.

The embryonic development at 23°C, proceeds as shown in Fig. 2.3.7 (Ohtsu *et al*., 2007). The embryos start the first division 3 hours and 15 minutes after light exposure, and develop through the morula and blastula stages to the planula stage by 12 hours after the light exposure. The planulae, ~170 µm long and ~130 µm wide, with 10 µm long cilia over their surface, swim in the water for about 2 days before settling on hard substrates, either of natural (*e.g*., pebbles, bivalve shells, wood) or artificial materials (*e.g*., ceramic, glass, various plastics) to metamorphose into the polyp stage (Kawahara *et al*., 2006).

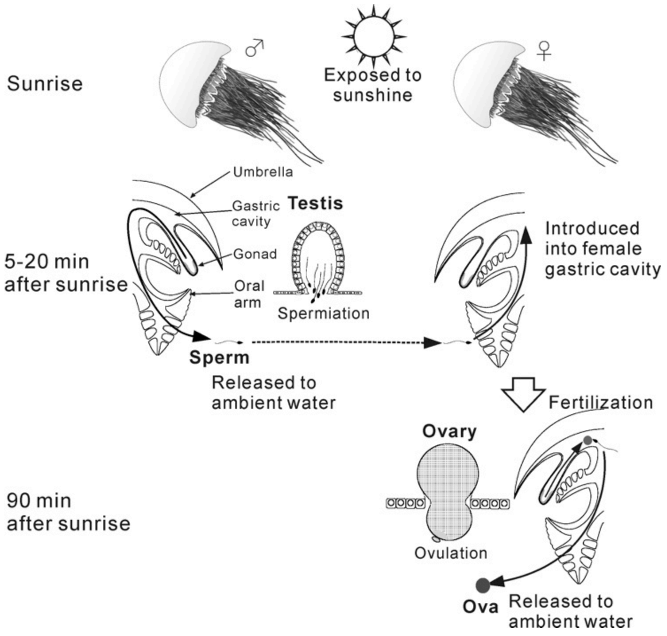


Fig. 2.3.6 Schematic diagram of spermiation and ovulation of *Nemopilema nomurai* induced by exposure to natural sunlight. Spermiation takes place 5–20 minutes after sunrise, and sperm released into ambient water may be introduced into the female gastrovascular cavity. Ovulation takes places approximately 90 minutes after sunrise, and eggs may be fertilized in the gastrovascular cavity and released to ambient water. Fertilization may also occur in the ambient water (drawn based on findings by Ikeda *et al*., 2011b).

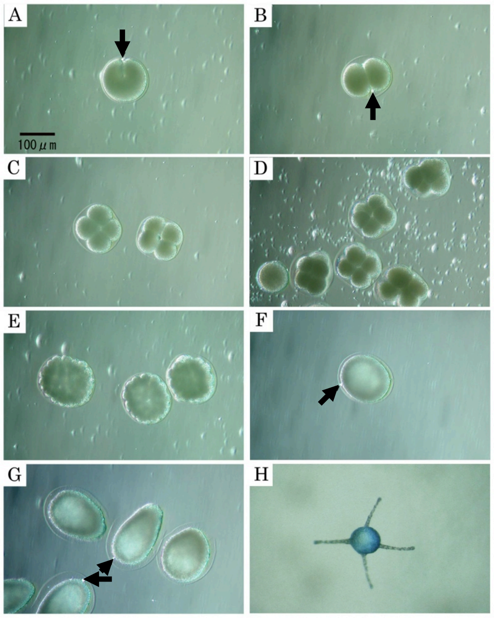


Fig. 2.3.7 Embryonic development of *Nemopilema nomurai* at 23°C with time after release. (A) 3 hours and 15 minutes: the first division begins at the animal pole (arrow), (B) 3 hours and 40 minutes: the first division occurs, (C) 4 hours and 20 minutes: the second division occurs, (D) 5 hours: the third division occurs, (E) 6 hours and 40 minutes: the morula stage is reached, (F) 9 hours: the blastra stage is reached, (G) 12 hours: the pear-shaped embryo is hatched into planula, and (H) 50 hours: the planula metamorphoses into a 4-tentacled polyp. Arrows indicate polar bodies (from Ohtsu *et al.*, 2007).

Asexual reproduction

At ~20°C, it takes 2 days for settled planulae to completely metamorphose into polyps (scyphistomae) with 4 tentacles and a calyx diameter of 250–300 µm. Young polyps develop in 6–10 days after settlement to an intermediate stage with 8 tentacles and calyx diameter of ~500 µm. Fully developed polyps with 16 tentacles and 800–1,100 µm calyx diameter are attained 10–20 days after settlement, when they start asexual reproduction by means of podocyst production (Fig. 2.3.8, Kawahara *et al*., 2006). A stolon protrudes from the bottom of the calyx and attaches to the substrate ~10–300 µm away from the base of the polyp. Then, the polyp body mass gradually moves to the new attachment site, leaving a podocyst behind at the former position. The newly produced podocysts are whitish and ~300 µm in diameter. New polyps can excyst from the podocysts after variable dormant periods up to 9 years (Uye *et al*., unpubl.). In the laboratory, a single very productive original (or founder) polyp formed a colony consisting of 18 podocysts and 6 polyps when kept at 18°C for 6 months (Kawahara *et al*., 2006).

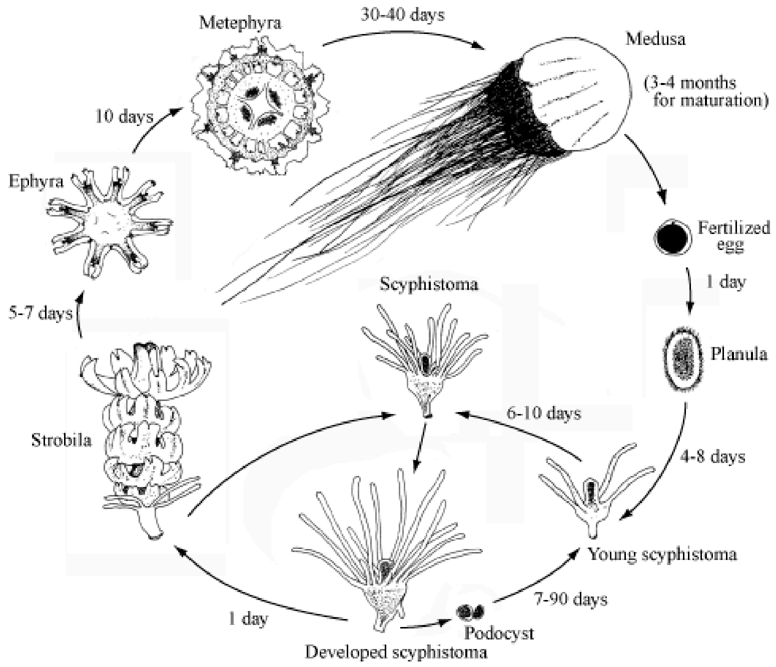


Fig. 2.3.8 Schematic representation of the life cycle of *Nemopilema nomurai* (from Kawahara *et al*., 2006).

In the laboratory, Kawahara *et al*. (2013) found polyps kept at temperatures ≥19°C never strobilated, but those kept at ≤15°C did; it took at least a month to start strobilation at 11°C and 15°C, and 3 months at 9°C (Kawahara *et al*., 2013). These results suggest that seasonal chilling can be a trigger to induce strobilation in wild polyps. When strobilation commences, the calyx becomes elongated and segmented; in 1.5 days rhopalia with statoliths become apparent, and in 2 days ephyral lappets start to elongate and pulsate rhythmically. Fully developed strobilae, 2.2–2.8 mm long from the base of the polyp to the top of the ephyral mouth, liberate ephyrae one by one into the water (Fig. 2.3.8). Five is the average number of ephyrae formed by strobilation (Kawahara *et al*., 2006).

Growth to the medusa stage

Newly released ephyrae are able to ingest food, such as *Artemia* nauplii, and grow at temperatures ≥18°C. However, they are unable to catch sufficient food to sustain net grow at ≤11°C. Therefore, seasonal warming, *i.e.*, ≥15°C, enables and accelerates the growth of ephyrae. At 22°C, approximately 10 days post-liberation, the ephyrae grow into metephyrae, with secondary lappets extending outwards to the primary lappets such that the bell margin looks polygonal and is 8–14 mm wide from lappet tip to lappet tip. The metephyrae have eight clearly defined oral arms, and each arm branches into two wings at the tip. In advanced metephyrae (14–18 mm wide; approximately 20 days post-liberation), a reddish filiform appendage develops at the junction point of the wings, and the central mouth is still open. After the central mouth has closed, the metephyrae advance to the medusa stage and grow to a bell diameter of 40–110 mm at 40–50 days post-liberation (Fig. 2.3.8). Numerous appendages are present on the oral wings and scapulets. In the barrier-free open sea, *N. nomurai* grow much larger, attain sexual maturity in late fall and early winter, and die off by mid-winter. Their planktonic life span is less than a year, but their benthic life span may be multiple years.

2.4 Phylum Cnidaria – Class Cubozoa

Cubomedusae are meroplanktonic jellyfish that can inflict painful to deadly stings, depending on the species. It is a relatively small group (>30 species) found in tropical and subtropical waters, with the greatest diversity occurring in Pacific waters. Each small polyp develops directly into one medusa (Fig. 2.4.1).

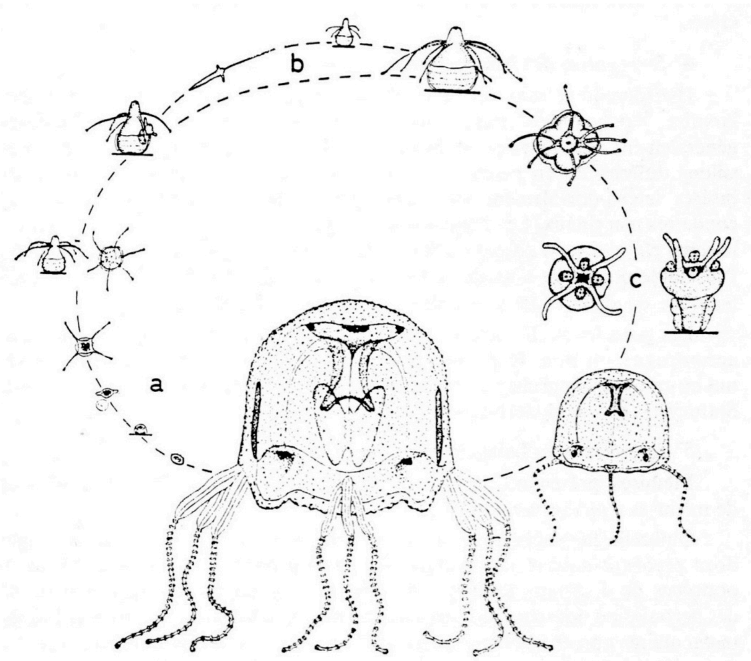
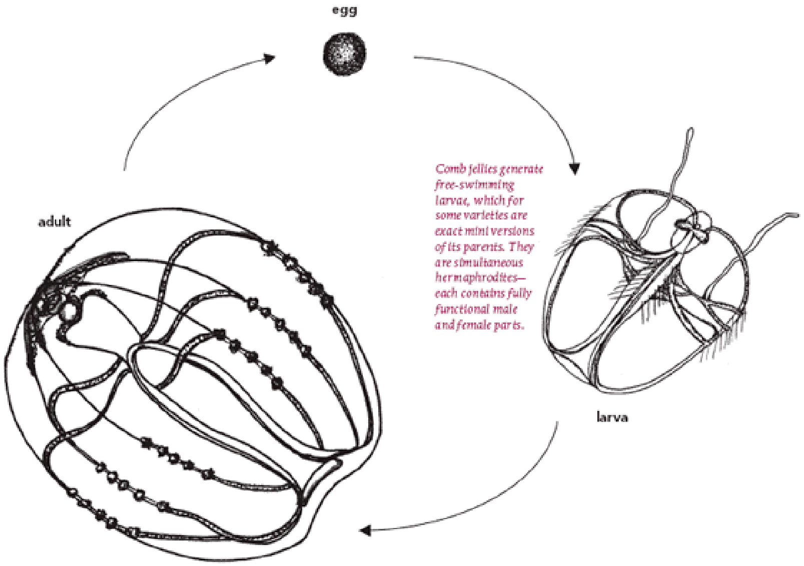


Fig. 2.4.1 Cubozoan life cycle (from Bouillon *et al*., 1993).

2.5 *Phylum Ctenophora*

Ctenophores, also known as comb jellies, are gelatinous zooplankton that are often grouped with medusae as “jellyfish”. However, they are in a different phylum (Ctenophora) and do not sting their prey. Although they are also gelatinous, they differ from the cnidaria in a variety of ways, such as using ciliated comb plates for locomotion. Photographs of several species present in the Salish Sea, such as *Pleurobrachia bachei* and *Beroe abysisicola,* are included in Wrobel and Mills (1998). Because they are so delicate, few of the >200 described species can be collected or preserved with standard methods. Five of the six orders of ctenophores (except the Order Platyctenida, which lives epiphytically on benthic animals) are holoplanktonic with the entire life cycle completed as plankton (Fig. 2.5.1). Most studied species are hermaphroditic, releasing eggs and sperm into the water, where fertilization produces larvae. All but one ctenophore order (Beroida) have two-tentacled larvae called cydippids which quickly grow and develop directly into adults. The larvae of beroid ctenophores, which lack tentacles like the adults, develop directly into adults.



Comb jellies generate free-swimming larvae, which for some varieties are exact mini versions of its parents. They are simultaneous hermaphrodites—each contains fully functional male and female parts.

Fig. 2.5.1 Ctenophore life cycle of the comb jelly *Mnemiopsis leidyi* (http://seagooseberries.weebly.com/detail.html).

2.6 Phylum Chordata – Class Thaliacea

Salps (Order Salpida), one of three orders in Class Thaliacea, are also often called "jellyfish". However, they are in a different phylum (Chordata) and are filter-feeders that eat pico-, nano- and microplankton. They are relatively large and can be collected with large nets and preserved by standard methods. Their holoplanktonic life cycle alternates between an asexually-reproducing colonial form and a sexually-reproductive solitary form (Fig. 2.6.1).

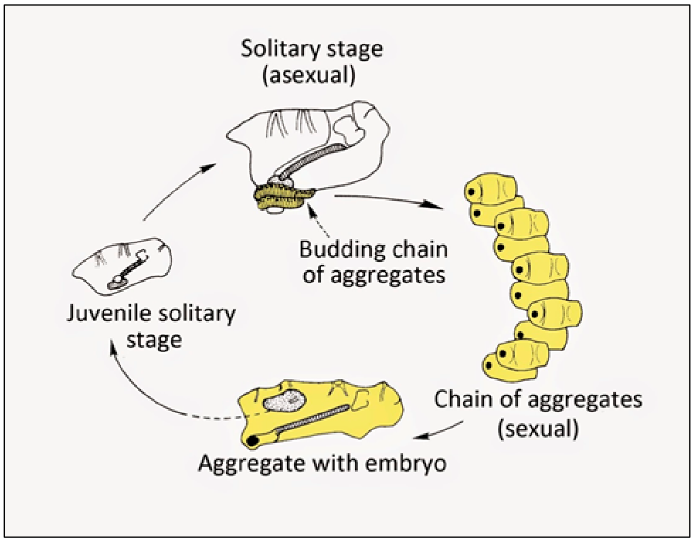


Fig. 2.6.1 Salp life cycle (from Alldredge and Madin, 1982).

3 Sampling Considerations

Shin-ichi Uye[1], Richard Brodeur[2], Haruto Ishii[3] and Alexander Zavolokin[4]

[1] Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Japan
[2] Northwest Fisheries Science Center, Hatfield Marine Science Center, National Marine Fisheries Service, NOAA, Newport, Oregon, USA
[3] Tokyo University of Marine Science and Technology, Tokyo, Japan
[4] Pacific Scientific and Research Fisheries Center (TINRO-Center), Vladivostok, Russia

3.1 Introduction

Data on the abundances, biomass, and spatio-temporal distributions of jellyfish are considered basic components needed to assess their population size as well as to understand their functional roles in the food chain dynamics and material cycling in the ocean. Traditional sampling gears (*i.e*., plankton nets and trawls) used to quantify robust zooplankton such as crustaceans (copepods and euphausiids) and fish (eggs and larvae) (Harris *et al*., 2000) are often inappropriate for jellyfish, due primarily to their fragility, leading to physical damage and serious undersampling (Mills, 2001; Raskoff *et al*., 2003; Purcell, 2009). In addition, the body size of some species is extremely large for regular net sampling, as in the example of the giant jellyfish *Nemopilema nomurai*, which have a maximum bell diameter of ~ 2 m. Moreover, their spatial distribution is often very patchy, as typically manifested by the moon jellyfish *Aurelia aurita* s.l., which form dense patchy aggregations (Hamner *et al*., 1994; Graham *et al*., 2001; Uye *et al*., 2003). Recognition of these shortcomings in net sampling has led to a variety of non-capture methods, including acoustic surveys, video observations, and aerial and ship sightings. Each survey has its own merits and demerits which are discussed below. Hence the selection of method(s) may depend on jellyfish species (body size, fragility and behavior), vertical range (shallow or deep), geographical scale (small inlet to open ocean), temporal scale (snapshot survey to long-term monitoring), and the research purpose to be achieved.

3.2 Net towing

In many regions of the North Pacific, much of our information on distribution and abundance trends through time comes from surveys for pelagic or demersal fishes using large fish trawls (Brodeur *et al*., 2002; Zavolokin, 2010, 2011; Suchman *et al*. 2012), although some information is also available from fine-mesh purse seines (*e.g*., Shenker, 1985). A number of these surveys are done annually and in some cases, multiple times per year, to assess fish abundance patterns. Although jellyfish are considered a by-catch in these surveys, quantitative information on species composition, abundance and biomass, and size composition is often recorded somewhat consistently through time.

In the California Current, much of the data comes from large pelagic trawl surveys on juvenile salmon and other pelagic fishes. Although the forward mesh sizes are quite large, these trawls generally have a fine-mesh liner in the rear of the net to retain small fishes. In some cases (Suchman and Brodeur, 2005; Suchman *et al.*, 2012), adjustments to the mouth area of the trawl have been made to include only the area of sufficiently fine mesh to retain most of the larger jellyfish (scyphomedusae and some larger hydromedusae). In the Gulf of Alaska and Bering Sea, trawl surveys are conducted for both demersal (Brodeur *et al.*, 2002; Decker *et al.*, 2014) and pelagic fishes (Cieciel *et al.*, 2009; Decker *et al.*, 2014). Based on observations using remotely operated vehicles (Brodeur, 1998), it is known that the predominant species of jellyfish are found primarily in the water column; therefore, the bottom trawl may only be sampling these taxa during the deployment and retrieval of the net. There is a need to intercalibrate between surface and bottom trawls fished in the same area at the same time to determine differences in catchability between these two trawling methods.

In Russian surveys, biomass and abundance of large jellyfish are estimated using data from trawl catches (Zavolokin, 2010, 2011). The main targets of these surveys are commercial species of fish, and jellyfish are considered to be a by-catch. Different types of pelagic trawls have been used in the 1990s and 2000s, with vertical and horizontal openings varying from 30 to 56 m and from 28 to 50 m, respectively. The trawls always are equipped with a small-mesh (1 cm) liner in the cod end, which allows relatively small jellyfish, with bell diameter $\geq$1 cm to be caught.

Due to the relatively high speed of the tows (from 3 to 5 kt), a significant proportion of jellyfish is extruded through the trawl meshes. Thus, a catchability coefficient is used to get more accurate estimates. The catchability coefficient is assumed to be 0.1, which means multiplying the catch by 10 to arrive at the estimated abundance or biomass (Zavolokin, 2010). However, there has not been any special research to determine this coefficient and it is unknown how it varies among species. Neverthless, such an approach is believed to give more accurate estimates because jellyfish biomass and abundance in trawl catches are greatly underestimated. Therefore, this makes for possible comparisons of these estimates of jellyfish biomass with estimates for fish and squids as well as plankton species that are important for ecosystem studies.

The biomass (abundance) of jellyfish was determined by:

$$B(N) = \frac{b(n)}{v \cdot t \cdot a \cdot \mathrm{k}}$$

where B (N) is the estimated biomass (abundance) of species in kg km^{-2} (ind. km^{-2}), $b(n)$ is the actual mass (abundance) of species in a catch in kg (ind.), v is the velocity of trawl towing in km h^{-1}, t is the duration of trawling in hours, a is the horizontal opening of the trawl mouth in km, and k is the catchability coefficient. More empirical research needs to be done to estimate catchability for different combinations of jellyfish size and mesh size, similar to the recent work of De Robertis *et al*. (2016) in the Arctic Ocean.

3.3 Acoustic instruments

Traditional surveys using plankton nets are problematic for studying jellyfish quantitatively, particularly large scyphozoan species because of their fragile body tissues in addition to sparse or uneven distributions (Hamner *et al.*, 1975; Graham *et al.*, 2001; Mills, 2001; Purcell, 2009). One of several alternative methods to estimate jellyfish distributions and abundances is to employ acoustic instruments, which have been routinely used to estimate fish abundances (MacLennan and Simmonds, 1992). Acoustics are most effective in detecting fish with gas-filled swim bladders, which yield a strong acoustic signal due to differences in density between gas bladders and the surrounding water. Jellyfish have been traditionally disregarded as conspicuous sources of sound scattering because of their high water content and, therefore, low density contrast with the surrounding water, probably causing their contribution to total backscattered acoustic energy to be masked by other zooplankton (Alvarez Colombo *et al*., 2003; Graham *et al*., 2010) or fish (De Robertis and Taylor, 2014). Nevertheless, recent studies have shown that many jellyfish species can scatter more sound per individual than most zooplankton and hence can be detected acoustically.

3.3.1 Multi-frequency echosounders

Scientific echosounders transmit sound pulses of several chosen frequencies, ranging usually from 18 to 200 KHz, to the water, and receive echoes backscattered from various objects in the water column and at the seabed. The acoustic echoes transmitted to echosounders can be used to detect aggregated or solitary jellyfish if their occurrence is confirmed by concurrent net samplings, and to estimate the density of them if the sound scattering characteristics of the target organisms, particularly target strength (TS), are known. TS is a measure of the proportion of echo energy intensity backscattered by the acoustic target, in this case a medusa, relative to the incident sound pulse. However, it is not easy to determine TS for a particular species because a sound scattering process varies with jellyfish species, size, shape, water content, and orientation in addition to frequency and incidence angle of acoustic pulse (Multu, 1996; Monger *et al*., 1998; Brierley *et al*., 2004; De Robertis and Taylor, 2014). The methods commonly used to estimate the TS of jellyfish are: 1) measurements on a tethered animal (Monger *et al*., 1998; Brierley *et al*. 2004; Hirose *et al*., 2009; Kang *et al*., 2014), 2) detections of an *in situ* single target (Mutlu, 1996; Brierley *et al*., 2001, 2005; Lynam *et al*., 2006), and 3) the use of models based on hydroacoustic physics (Chu *et al*., 2003; Demer and Conti, 2003; Graham *et al*., 2010). The advantages of using scientific echosounders are that they can sample large volumes of water in a relatively short time and provide estimates of abundances, biomass and spatial distributions of jellyfish. One of the most extensive acoustic surveys was conducted in the Namibian Benguela Current (~1400 km long), where the geographical distribution in biomass of two jellyfish species, *Chrysaora hysoscella* and *Aequorea forskalea*, and pelagic fishes including Cape horse mackerel, Cape hake and clupeids were investigated (Lynam *et al*., 2006).

One of the initial studies using scientific echosounders in the PICES region was conducted in the innermost part of Tokyo Bay where aggregations of *Aurelia aurita* s.l. were detected with a multifrequency (50 and 200 kHz) sonar (Furuno Co., FQ-50) combined with simultaneous plankton net tows to confirm this species existence (Inagaki and Toyokawa, 1991). Later, using the same technique, Toyokawa *et al*. (1997) detected circular to elliptical aggregations (longest dimension: 790 m) of *A. aurita* s.l. through an approximate 20-m water column. In the U.S., in order to assess the availability of jellyfish prey resources for leatherback turtles (*Dermochelys coriacea*) foraging off central California, acoustic investigations were performed to estimate the abundance and distribution of scyphozoan jellyfish, *i.e.*, *Aurelia* spp., *Chrysaora colorata, C. fuscescens* and *Phacellophora camtschatica* with a Simrad EK-60 echosounder at 38 and 200 kHz (Graham *et al*., 2010). Using a model-determined TS, an algorithm was developed to extract jellyfish echoes from total acoustic backscatter, and then mean numerical density was estimated with an echo-integration technique to be 0.003 jellyfish m^{-3} over the survey area. In

Russia, the most extensive acoustic survey of jellyfish was conducted in shelf waters along western Kamchatka (~1000 km long), where a Simrad EK-500 echosounder was operated at 38 and 120 kHz, with occasional trawl samplings of scyphozoans (*Aurelia limbata, Chrysaora melanaster* and *Cyanea capillata*) and hydrozoans (*Aeginura grimoldii*) to determine their TS, and subsequently their geographical distributions (Fig. 3.3.1, Gorbatenko *et al*., 2009). According to these hydroacoustic measurements, total abundance and biomass of all jellyfish species in waters off west Kamchatka were 193.7 million individuals and 1,672,700 tons, respectively. Because of larger body size and hence stronger TS of the giant jellyfish *Nemopilema nomurai*, which have been blooming recurrently in the East Asian Marginal Seas, high resolution echograms collected by a Simrad EK-60 (38, 120 and 200 kHz) operated at appropriate conditions (*e.g*., pulse duration: 0.128–0.256 ms, ping interval: 0.2 s, ship speed: 5 kt) could detect individual medusae (Sadayasu *et al*., 2009; Matsuura *et al*., 2014). This technique was also used to investigate the density and vertical and horizontal distributions of this jellyfish species (Lee *at al*., 2007, 2010; Sadayasu *et al*., 2009).

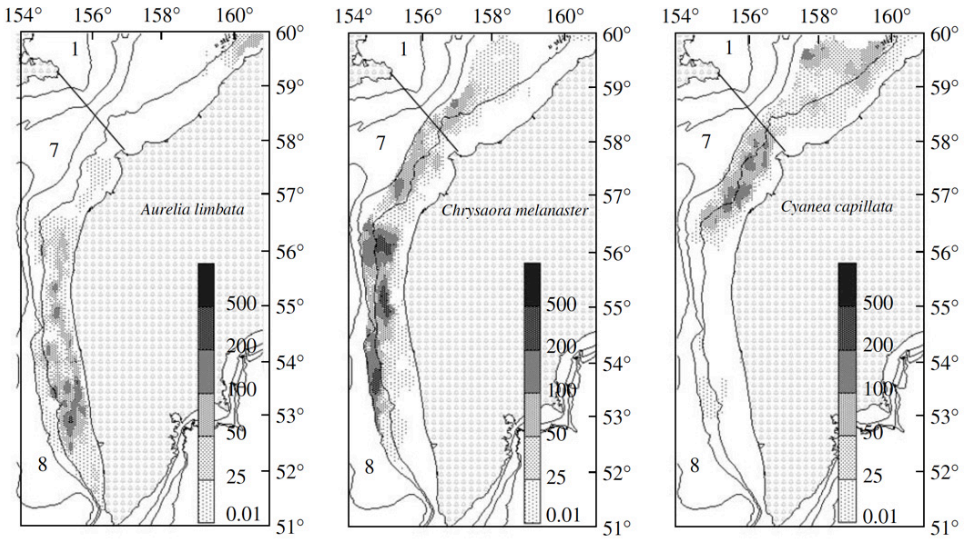


Fig. 3.3.1 Geographical distribution of biomass (tons mi^{-2}) of *Aurelia limbata* (left), *Chrysaora melanaster* (middle) and *Cyanea capillata* (right) off west Kamchatka in June–July 2005, according to hydroacoustic measurements (from Gorbatenko *et al*., 2009).

3.3.2 Dual-Frequency Identification Sonar

Dual-Frequency Identification Sonar (DIDSON; Sound Metric Co.), or an acoustic camera, is a high-definition imaging sonar that provides near-video-quality images of underwater objects. The DIDSON transducer operates at megahertz frequencies, *i.e*., 1.0 or 1.8 MHz, and projects an azimuthal composite beam consisting of 96 fan-shaped narrow beams, each having two-dimensional angular resolution of 0.3° by 14°, to create an overall field of view of the composite bean of 29°. When transmitting vertically (*i.e*., 90° to the water surface), the field of view is defined by the height (or down range: D, m) and the rectangular base area (0.5D m × 0.25D m), as schematically depicted in Fig. 3.3.2.

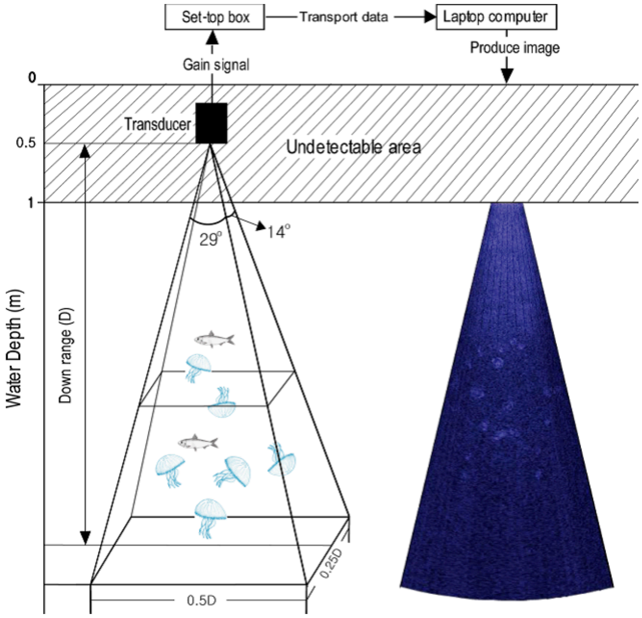


Fig. 3.3.2 Schematic representation of the pyramid-shaped sonar view field (left), and a sonar image from the DIDSON (right) operated in high frequency mode (1.8 MHz). The upper 0.5 m depth is undetectable view field (from Han and Uye, 2009).

A DIDSON was used to monitor the abundance, size, and swimming behavior of fish, particularly anadromous fish (*e.g*., salmon) in rivers (Tiffan *et al*., 2004; Holmes *et al*., 2006; Handegard and Williams, 2008). A preliminary use of this machine in jellyfish studies was conducted to detect individual medusae of *Nemopilema nomurai* and their vertical distribution in coastal waters of Japan (Honda and Watanabe, 2007) and the Yellow Sea (Lee *et al*., 2010). Han and Uye (2009) used the DIDSON for the first time to determine the spatial distribution and population abundance of scyphozoan jellyfish (*i.e*., *Aurelia aurita* s.l. medusae in a brackish-water lake of the Honjo area (area: 16.2 km^2, average depth: 5.1 m), Honshu, Japan (Fig. 3.3.3). During the survey, the transducer was mounted on a wooden frame secured to a boat which ran at a speed of 0.7–0.9 m s^{-1} along three near-parallel transects (total distance: 12 km) and the images were saved in a computer at a rate of 10 frames s^{-1} for later review. As the archived sonar images at a high-frequency mode (1.8 MHz) provided sufficient resolution to detect individual medusae, their numbers at various depths, except for the near-field dead zone (<0.5 m from the transducer), could be counted and their horizontal (Fig. 3.3.3) and vertical distributions determined. Hence, this instrument is very useful for the accurate quantification of relatively large jellyfish in relatively shallow waters, since it has mechanical limits of size detection (bell diameter: ≥ 5 cm) and depth penetration (maximum depth: 12 m at 1.8 MHz). In order to monitor jellyfish occurrence at longer temporal scales, the DIDSON can provide much more accurate and reliable information than conventional net sampling, although net captures remain necessary to determine the body size composition of the medusa population (Makabe *et al*., 2012).

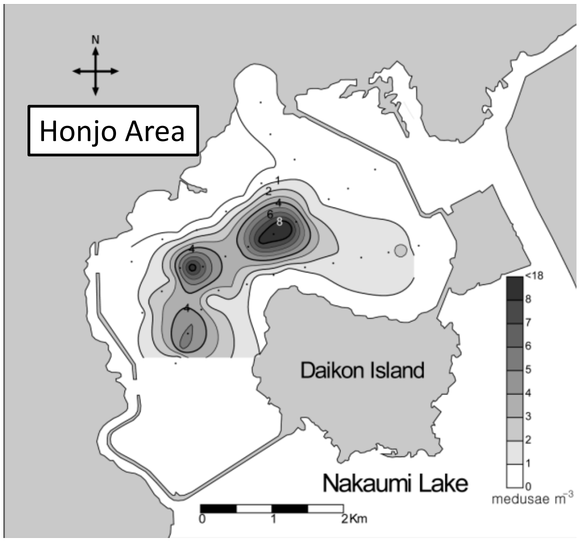


Fig. 3.3.3 Contour map showing the geographical distribution of *Aurelia aurita* s.l. in Nakaumi Lake in the Honjo area, Shimane prefecture, August 29, 2007. The gridding method was employed based on medusa densities at 30 GPS stations (denoted by dots) (from Han and Uye, 2009).

3.4 Video observations

Video observations from towed instruments, moorings, or attached to autonomous underwater vehicles (AUV), remotely-operated vehicles (ROV) or manned submersibles are useful for providing visual data of jellyfish, even in small-scale aggregation patterns (Purcell *et al*., 2000; Toyokawa *et al*., 2003) or in areas where general net sampling is not feasible (*e.g*., deep sea, Larson *et al*., 1992; Lindsay *et al*., 2004; Lindsay, 2005). There is often good agreement with overall densities determined with video and net sampling (Purcell, 2009).

Data on the vertical distribution of large jellyfish in the eastern Bering Sea are more limited since the trawls used generally fish only a single layer quantitatively. However, detailed *in situ* observations have been made using underwater video cameras on ROV. Brodeur *et al*. (2002) showed that the five most dominant jellyfish species observed in the videos were distributed primarily between 15 and 40 m in the water column, although some *Chrysaora* were found as deep as the observations were made (95 m). Both acoustic and video observations showed that the jellyfish (primarily *C. melanaster*) had a shallower distribution at night than during the day (Brodeur, 1998).

Large blooms of *Aurelia aurita* s.l. medusae are frequently observed in the innermost part of Tokyo Bay, Japan, usually in dense patchy aggregations such that traditional net sampling usually leads to underestimation of their population abundance (Ishii, unpubl.). Underwater video systems can determine not only the abundance and the bell diameter of medusae, but also the vertical distribution of medusae when the systems are deployed from the surface to the bottom in the center of an aggregation (Fig. 3.4.1). Hence, by determining the horizontal dimension of the medusa aggregation near the surface by sighting from a boat with a GPS navigation system, one can estimate the total abundance of medusae contained in the aggregation. These numerical data can also be converted to biomass data if the bell diameter and body mass (wet, dry or carbon weight) relationship has been obtained in advance. If all aggregations of medusae in the survey area are found and measured, the average abundance and biomass of the *A. aurita* s.l. medusa population can be estimated.

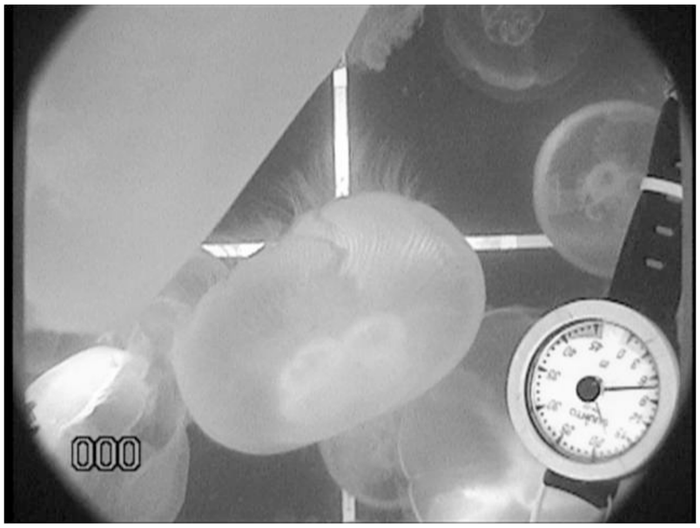


Fig. 3.4.1 A video frame grab showing *Aurelia aurita* s.l. from an underwater video system with a depth meter deployed in the innermost part of Tokyo Bay (unpubl. figure from H. Ishii).

3.5 Aerial and ship sightings

Sighting with the naked eye is the simplest method to survey relatively large marine animals such as pinnipeds (Thompson *et al*., 2001), cetaceans (Forcada *et al*., 2004) and seabirds (Gilchrist and Mallory, 2005), and this simple method is also applicable to study jellyfish which occur near the sea surface. For systematic surveys of jellyfish over relatively wide geographical ranges, it is necessary to use observation platforms, primarily aircraft (aerial sighting surveys) and ships of opportunity (ship sighting surveys).

3.5.1 Aerial surveys

Aerial surveys using aircraft have been performed to determine the number of aggregations or individuals of jellyfish in the top few meters of the water column. Purcell *et al*. (2000) used this technique to determine the number of *Aurelia labiata* aggregations in Prince William Sound, Alaska, for 3 consecutive years, and found marked inter-annual variations in the aggregation number. A similar survey was conducted in the western Inland Sea of Japan in 2000, when *Aurelia aurita* s.l. formed dense aggregations (Uye *et al*., 2003). In their study, composite air photographs taken from a plane combined with a ground-truthed net survey revealed that the aggregations, which looked cloud-like, covered an area of 2.34 km^2 and contained at least 5.83×10^8 individuals or 9.36×10^4 metric tons wet weight of medusae (mean bell diameter: 14.6 cm) along approximately 100 km of coastline (Fig. 3.5.1). The size and characteristics of aggregations of *Aurelia* sp. in the Huon Estuary, southern Tasmania, Australia, were also investigated using a combination of aerial photographs and underwater videos taken by divers (Crawford *et al*., 2011). Aerial surveys can also detect individual medusae if their body size is large enough to give discrete images. For example, Graham *et al*. (2003) obtained photographic images of an extensive bloom of *Phyllorhiza punctata* (bell diameter: ≥30 cm) in the northern Gulf of Mexico, and counted them individually from discrete images as well as from images of overlapping medusae by application of a proper conversion. Further, Houghton *et al*. (2006) were able to count from an airplane at altitude of 152 m three large jellyfish species, *i.e.*, *Rhizostoma octopus, Cyanea capillata* and *Chrysaora hysoscella* (bell diameter or body length: ≥1 m) separately in the southern Irish Sea. Individual counting of *Nemopilema nomurai* (bell diameter: ≥1 m) in the coastal waters of Japan was also possible from an aircraft at an altitude of ~200 m (Uye, unpubl.).

Fig. 3.5.1 An aerial photograph of *Aurelia aurita* s.l. aggregations spread over an inlet of the western Inland Sea of Japan on August 24, 2000 (from Uye *et al*., 2003).

Although aerial surveys are greatly superior to ship surveys in the ability to gather data over a vast geographical range for a much shorter time, they are subject to more limitations such as sea state, visibility and observer bias (Houghton *et al*., 2006).

3.5.2 Ship surveys

Visual monitoring of jellyfish from ships of opportunity has been carried out since the turn of this century, when jellyfish blooms appeared to become more frequent and extensive in many parts of world oceans (*e.g*., Sparks *et al*., 2001; Doyle *et al*., 2007; Albert, 2009; Bastian *et al*., 2011; Randriarilala *et al*., 2014). For example, Sparks *et al*. (2001) counted two jellyfish species, *Chrysaora hysoscella* and *Aequorea aequorea*, from a research vessel steaming in the Namibian shelf waters, one of the world-renowned productive fisheries grounds but affected recently by dramatic increases of jellyfish populations (Lynam *et al*., 2006). The monitoring revealed that both species displayed marked patchiness, but showed a different geographical distribution from each other; *C. hysoscella* was found inshore whereas *A. aequorea* tended to be found offshore. Doyle *et al*. (2007) and Bastian *et al*. (2011) visually counted five jellyfish species (*i.e*., *Aurelia aurita* s.l., *Chrysaora hysoscella*, *Cyanea capillata, C. lamarckii* and *Rhizostoma octopus*) from ships of opportunity traversing the Irish and Celtic seas, extensive shelf waters where no systematic surveys on jellyfish had previously been performed, and found that each species had its own geographical distribution and seasonal occurrence.

Sighting surveys from either ships or aircraft (see above) always have limitations, such as dependency on weather, the restriction to large and easily identified species present near the surface during daytime, the lack of information on physico-chemical environmental variables (except for ships equipped with a monitoring system), accurate jellyfish size composition, and the total densities and biomass of jellyfish in the water column. However, sighting surveys using ships of opportunity provide a reliable cost-effective tool to monitor the spatial and temporal distributions of jellyfish across continuous transects. If the data are accumulated over several years, these surveys can constitute invaluable local baseline and time series to investigate the mechanisms that cause outbreaks as well as inter-annual variations of jellyfish populations. In Japan and Korea, where coastal fisheries have been affected often in the last two decades by outbreaks of the giant jellyfish *Nemopilema nomurai*, systematic monitoring has been performed to forecast the possible outbreaks of this species to alleviate the damage. In Japan, a visual count of young medusae en route from their seeding and nursery ground in Chinese waters to Japanese waters has been carried out along ferry routes between Japan and China since 2006 (Uye, 2010, 2013; see also section 7). Based on the average medusa density in June and July over the Yellow Sea, a bloom forecast is possible so that fishermen can prepare for jellyfish encounters 1–3 months prior to their occurrence in Japanese coastal waters. In Korea, sight survey monitoring from ships of opportunity has been used extensively over its exclusive economic zone to gather information on the occurrence of *N. nomurai* in order to forecast the bloom intensity and analyze seasonal and yearly variations of its population size and geographical distribution (Yoon *et al*., 2014).

4 Spatio-Temporal Variations of Biomass and Bloom Conditions in Regional Seas

Jellyfish spatio-temporal variations of biomass and bloom conditions of cnidarians and ctenophores for different PICES regions are described next, starting counterclockwise around the North Pacific with the west coast of the United States.

4.1 West Coast of United States

Richard D. Brodeur[1] and John C. Field[2]

[1] Northwest Fisheries Science Center, Hatfield Marine Science Center, National Marine Fisheries Service, NOAA, Newport, Oregon, USA
[2] Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Santa Cruz, California, USA

4.1.1 Introduction

The West Wind Drift, or Subarctic Current, flows across the North Pacific and then bifurcates off North America to form the Alaska Current that flows to the north and the California Current that flows to the south, from southern British Columbia to Baja California, Mexico, from approximately 50°N to 30°N. Mixing occurs between oceanic waters and those from the north and south, and these water masses are subsequently modified by coastal processes, such as runoff and upwelling in this eastern boundary current. Within the California Current, the focus of this section, Schwing *et al*. (1998) delineated three geographical regions based on wind stress which include: 1) the northern region (42–48°N) where wind stress varies from poleward to equatorward, 2) the central region (34–42^{o}N) with strongest wind stress, mainly equatorward, and 3) the southern region (22–34°N) where wind stress is predominantly to the south.

The northern transitional region is highly dynamic and ocean conditions fluctuate widely over time and space. The region has distinct seasonal as well as interannual and interdecadal fluctuations. Coastal upwelling along the coast is episodic off Oregon during the summer, but more persistent off northern California. During the upwelling season, a coastal jet is formed and dynamic frontal zones sometimes extend far out to sea as jets. In the winter, off the coasts of Oregon and Washington, the California Current either moves offshore or is replaced by the poleward flow of the Davidson Current. The California Undercurrent is a subsurface poleward current generally confined to the continental slope and most intense during the summer (Hickey, 1998). During El Niño events, the equatorward flow of the California Current is anomalously weak, and southern water intrusions move into the region. Thus, interannual variations in the northern California Current are likely to result from both regional and global-scale processes (Landry *et al*., 1989; Hickey, 1998). Interdecadal fluctuations with periods of 15–25 years have also been documented in the North Pacific and in the coastal transition region (Hare and

Mantua, 2000). These are based on variations in sea surface temperatures and abrupt changes in the survival or species composition of pelagic animals, such as occurred in 1977 and 1989.

The oceanography of the southern California Current varies considerably compared to that of the northern California Current (*e.g.*, Oregon and Washington coastlines) in a number of ways, several of which have high relevance to pelagic jellyfish abundance and distribution. In the northern California Current, strong seasonal upwelling winds and a relatively smooth coastline leads to the development during the spring and summer of a strong coastal jet over the continental shelf, with variable but typically strong seasonal upwelling supporting high productivity inshore. As the coastal jet develops around Cape Blanco (Oregon), Cape Mendocino (California) and other features farther south, the jet, as well as the offshore flow in the California Current, begins to exhibit higher eddy kinetic energy, leading to a more complex mesoscale regime of jets, eddies and meanders due to coastal geomorphology and complex bathymetry. Strong upwelling centers are located adjacent to headlands; important regions of enhanced primary productivity occur downstream of these sites, many of which are characterized by substantial mesoscale (and finer scale) eddy activity and complex circulation patterns (Strub *et al*., 1991; Steger *et al*., 2000). For example, along the central California coast Largier *et al*. (2006) showed that upwelling centers are characterized by high-nutrient low-chlorophyll waters with high chlorophyll waters located downstream from the upwelling center. Furthermore, upwelling “shadows” exist along the coast in the lee of coastal headlands and capes. Here, alongshore flow is reversed and the retained water contains high concentrations of chlorophyll and zooplankton (Graham *et al*., 1992; Graham and Largier, 1997; Steger *et al*., 2000; Largier *et al*., 2006). These habitats are among the most important habitats for large pelagic Scyphomedusae in this region. For example, in the Gulf of the Farallones, the upwelling shadow includes one of the widest areas of the continental shelf between Cape Blanco, Oregon (43°N) and Point Conception, California (34° 30′N) such that there are approximately 50 km between shore and the shelf break in this region relative to a coastal average closer to 20 km throughout most of the remaining coastline (Steger *et al*., 2000). Similarly, Monterey Bay, California, is a widely recognized productive region for Scyphomedusae (among other organisms) due to its retentive circulation patterns and complex bathymetry (Graham and Largier, 1997).

4.1.2 Spatial and temporal variations in jellyfish species composition and biomass

Wrobel and Mills (1998) provide an overview of most gelatinous taxa found along the west coast. One of the first studies to document gelatinous zooplankton from the northern California Current was the review of pelagic animals caught off Oregon from 1960 to 1968 by Pearcy (1972). He listed 33 Hydrozoa, 5 Scyphozoa, 2 Ctenophora, 1 Larvacea, and 8 Thaliacea taxa collected during this period. Coelenterates had the second highest biomass after Copepoda of all the major zooplankton groups, exceeding even Euphausiacea, and salps had the fifth highest biomass overall, reflecting their importance in this region. Hubbard and Pearcy (1971) described the geographic, seasonal and interannual variation of the six dominant species of salps (Thaliacea) collected from 1961 to 1964 and related them to environmental variables. *Salpa fusiformis* was found to be the most eurythermal species and was found in almost every month of sampling. However, during the El Niño year of 1963, its abundance was much lower, but some warm-water southern species (*Thetys vagina* and *Thalia democratica*) occurred only in that year, and became the numerically dominant taxa. Although depth-discrete sampling was made down to 1000 m, all salps were collected in the upper 150 m (Hubbard and Pearcy, 1971).

Scyphomedusae were analyzed from 263 fine-mesh purse seines made in the surface waters off Oregon and Washington from May–August, 1981 (Shenker, 1984). *Chrysaora fuscescens* were the numerically dominant species and occurred in > 82% of the collections made, followed by *Aurelia aurita* s.l. (24.3%) and *Cyanea capillata/Phacellophora camtschatica* (22.4% combined). Densities of *C. fuscescens* were highest in a narrow band close to shore, especially during strong upwelling periods. Based on changes in bell diameter, *C. fuscescens* grew rapidly in the summer months from a mean size of 8.6 cm in May to 18.5 cm in August. *Aurelia aurita* s.l. (5–45 cm diameter) generally were less abundant later in the summer and were found mostly between 10 and 15 km from shore. Pearcy *et al*. (1985) contrasted similar purse seine collections of gelatinous zooplankton from a strong upwelling year (1982) with that of an El Niño year (1983) and found that the frequency of occurrence of most large medusae, with the exception of *A. aurita* s.l., decreased in the second year. The dominant salp *Salpa fusiformis* was present only in 1982 whereas the more southern species *Thetys vagina* occurred only during the anomalous El Niño year. Heitstuman (1994) searched for medusae offshore in Oregon by SCUBA diving and found few specimens during the 1993 El Niño, which were more apparent during the more normal summer of 1994.

Extensive fine-mesh surface trawl collections (n = 365) from June and August of 2000 and 2002 from central Oregon to northern California were characterized for medusae by Suchman and Brodeur (2005). The dominant species caught were the schyphozoans *C. fuscescens* and *A. labiata* followed by *Phacellophora camtschatica* and the hydrozoan *Aequorea* spp. *Aequorea* spp. showed the highest frequency of occurrence overall due to its broad cross-shelf distribution, but *C. fuscescens* and *A. labiata* were substantially more important in terms of biomass, especially at nearshore stations. *Phacellophora camtschatica* was important in terms of biomass only during the August cruise, mainly in the southern part of the sampling area. There were no day–night differences in catch based on some limited diel sampling (Suchman and Brodeur, 2005). Suchman and Brodeur (2005) suggested that mesoscale physical features such as eddies and fronts may affect the distribution patterns of these weak-swimming organisms, leading to dense aggregations at convergent zones. There also seemed to be some larger scale habitat partitioning among the dominant jellyfish species.

The interannual and seasonal variation in large medusae abundance from eight years (2000–2007) of 1,746 surface trawl collections off Oregon and Washington were analyzed by Suchman *et al*. (2012). *Chrysaora fuscescens* and *Aequorea* spp. were caught in a similar proportion of the trawls (42% and 40%, respectively) but the abundance of the former, which peaked later in the summer, was an order of magnitude higher than the latter, which had a June peak in density. *Chrysaora fuscescens* tended to occur mainly at the innermost stations along each transect while *Aequorea* spp. were more broadly distributed with their center of abundance farther offshore. Both species, as well as *A. labiata*, increased in bell diameter from May through September although their patterns were different. Including more months and years in the analysis (Fig. 4.1.1), *C. fuscescens* showed an increase in modal length from April to August, but a subsequent decrease in September and October. Whether this is due to shrinkage because of less food availability or to a preferential mortality of the larger individuals is not known. *Aequorea* spp. showed a more bimodal size distribution pattern with a moderate increase in the main smaller mode but with a second mode appearing in late summer and even persisting until April (Fig. 4.1.1). This pattern is not likely to be caused by more rapid growth but instead may indicate a different population or species occurring in this region, perhaps of more offshore distribution that may have been advected onshore with the relaxation of upwelling.

Brodeur *et al*. (2008a, 2014) examined the spatial overlap of the dominant jellyfish with important pelagic fish species in the northern California Current. They found several fish species (particularly juvenile salmon and smelt) had relatively high overlap with *C. fuscescens* and to a lesser extent with *A. labiata* off southern Oregon (Brodeur *et al*., 2008a). Using a longer (13 years) time series of catches of *C. fuscescens* and herring, anchovy and sardines, Brodeur *et al*. (2014) showed that the spatial patterns of the centroids of abundance and spatial overlap were highly variable among the fish and medusae during June and September. The three forage species showed inverse relations of abundance to the jellyfish abundance in both months. Ruzicka *et al*. (2016) showed that juvenile salmon off Oregon and Washington had a high spatial overlap with *C. fuscescens* and showed an inverse relationship between their survival and jellyfish biomass. Taken together with food web modeling results (see section 6.3), it is suggested that the presence of a large number of jellyfish in the coastal zone may have a negative impact on the availability of habitat for fish as well as negative consequences for fish.

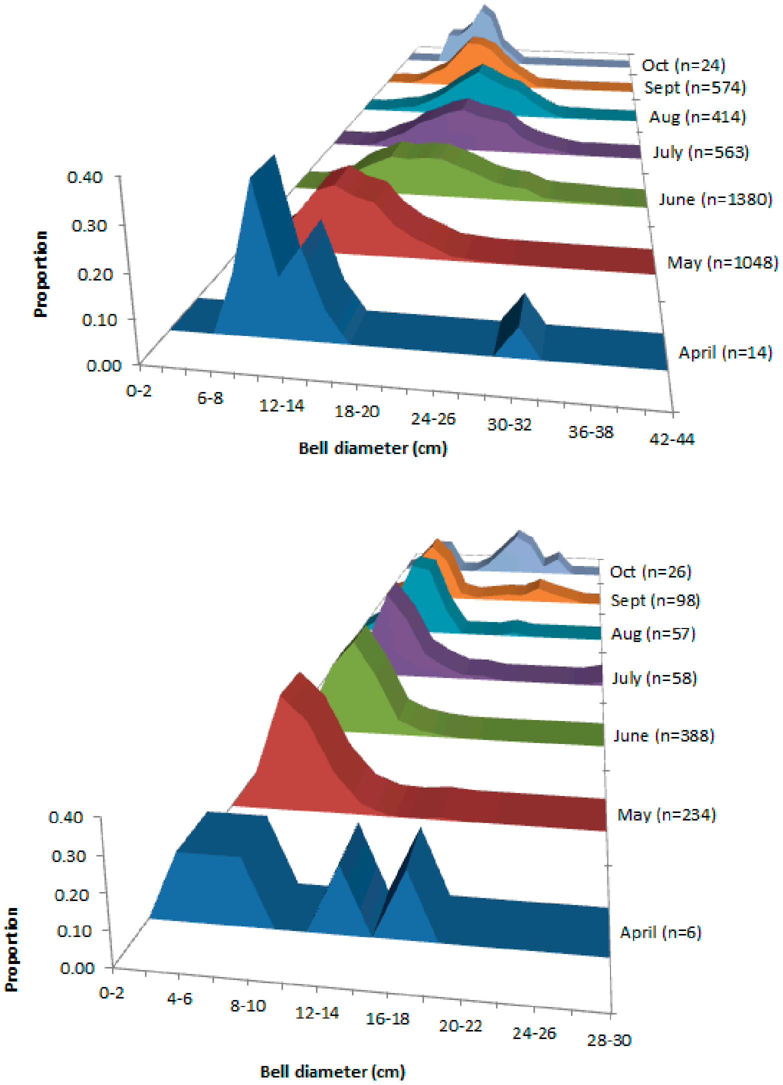


Fig. 4.1.1 Bell diameter frequency for *Chrysoara fucescens* (top) and *Aequorea* spp. (bottom) by month for seasonal collections off Oregon and Washington from 2001–2009. The sample size for each month is given in parentheses (from Suchman *et al*., 2012).

Very little is known about the benthic or early larval stages of medusae in the northern California Current. In an underwater survey of hard structures in Yaquina Bay, Oregon, Heitstuman (1994) found only a few occurrences of of *A. aurita* s.l. polyps, mostly on the undersides of man-made structures (jetties and piers), and no *C. fuscescens* polyps were found despite extensive searching. Molecular techniques were used to identify the scyphistomae of medusae in Coos Bay in southern Oregon and the specimens that were sequenced were all identified as *A. labiata* (Conley, 2013).

In the coastal (and to a lesser extent, offshore) waters of the southern California Current, the most commonly encountered and conspicuous members of the scyphozoan community in near surface waters include *C. fuscescens*, *C. colorata* and *A. labiata*. Relatively little research has been focused on the role of these species in this ecosystem, although Graham (1994) conducted a rigorous evaluation of the distribution and behavior of swarms of *C. fuscescens* in Monterey Bay relative to persistent hydrological features (upwelling shadows) and the swimming behavior that led to the characteristic swarms commonly encountered in coastal regions of the southern California Current. The life histories of these (and other) species have also been rigorously evaluated by a combination of field and aquarium studies (*e.g.*, Widmer, 2005, 2008). Some of the data from Graham (1994) was derived from an ongoing survey of juvenile rockfish and other micronekton in central California waters (Lenarz *et al.*, 1995; Sakuma *et al.*, 2007; Ralston *et al.*, 2013) from which data on the abundance of the three scyphozoan species listed above have been quantified for most of the time period between 1990 and 2012. These data form the foundation of most of what is available with respect to spatial-temporal variability in the abundance of scyphomedusae in these waters. Relatively little data are available for most other pelagic species.

A NOAA Fisheries survey has been conducted since 1983 in the waters off the central California coast (approximately 36° to 38°N) during the spring (May–June) upwelling season, and from the U.S./Mexico border to Cape Mendocino since 2004, to sample the abundance and distribution of young-of-the-year rockfish and other groundfish. The survey uses a modified Cobb midwater trawl (26-m headrope length) at 30-m headrope depth. Although not the target of the survey, jellyfish have been integral to it since its inception as sampling patterns have been adapted to abandon some stations, and routinely conduct short exploratory tows in others, to avoid tows in which high jellyfish catches damage the net or make meaningful enumeration of a given catch impossible (Ralston *et al.*, 2013). Data on the species composition and abundance of the three most frequently encountered large scyphozoans (*C. fuscescens*, *C. colorata* and *A. labiata*) have been collected reliably since 1990 (occasionally before then), with the exception of the years 2002–2004, and have begun to yield insights regarding the distribution, year-to-year variability and ecosystem interactions of these species in this region.

With respect to scyphozoan distribution patterns, Santora *et al*. (2012) evaluated 20 years of abundance data from the NOAA survey to evaluate distribution and species association patterns of a suite of marine micronekton (juvenile groundfish, forage fishes, krill, squid and jellyfish) off central California. They found that mesoscale variability of ocean conditions is the principal driver behind the spatial organization of the micronekton assemblages, with regions of species assemblages correlated to physical factors, latitudinal differences and the influence of localized upwelling and retention patterns. For example, the retention areas north and south of Point Reyes typically included high numbers of Scyphomedusae (primarily *C. fuscescens*), resulting in strong loading with respect to spatial overlap patterns. This spatial overlap suggests that there may be potential competition between jellyfish and other animals that feed on zooplankton, such as juvenile salmon as suggested in the northern California Current (Brodeur *et al.*, 2008a, 2014; Suchman *et al.*, 2008) and elsewhere (Cieciel *et al.*, 2009). In other words, jellyfish distribution patterns, like those of other micronekton in this ecosystem, are largely defined by bathymetric and physical patterns, with centers of upwelling and relaxation leading to distinct micronekton assemblages (Graham, 1994; Graham *et al*., 2001; Santora *et al*., 2012).

Due to the large-scale biogeographic features and circulation patterns described earlier, the central California region also appears to be the region of greatest relative abundance of these scyphozoan species as well, as illustrated by mean catch rates over the broader southern California Current survey range using data available from 2005–2012 (Fig. 4.1.2). This figure clearly shows that, at least during May–June, the two more abundant species, *C. fuscescens* and *A. labiata*, have their greatest relative abundance in nearshore central California waters, particularly the Gulf of the Farallones and Monterey Bay, with *A. labiata* more frequently found in offshore waters to the north and south of this region. The third species, *C. colorata*, a solitary rather than swarming species, is considerably rarer than the first two, but is more frequently found in offshore waters. A different survey using a high speed surface trawl during daytime hours to catch juvenile salmon (in late summer and fall time periods) led to comparable results, with *A. labiata* again tending to be more frequently encountered outside of the retention areas and in more offshore waters (Harding *et al*., 2011; J. Harding, unpubl. data). This is consistent with some of the results reported in Graham (1994) who found that the distance from shore of *Chrysaora* swarms in Monterey Bay tended to increase modestly during the non-upwelling period (fall and winter) relative to the upwelling season from which most of these survey data are described, although the increase in distance from shore for *Chrysaora* was not substantial and the variability in the distance from shore may have increased during the fall and winter as well.

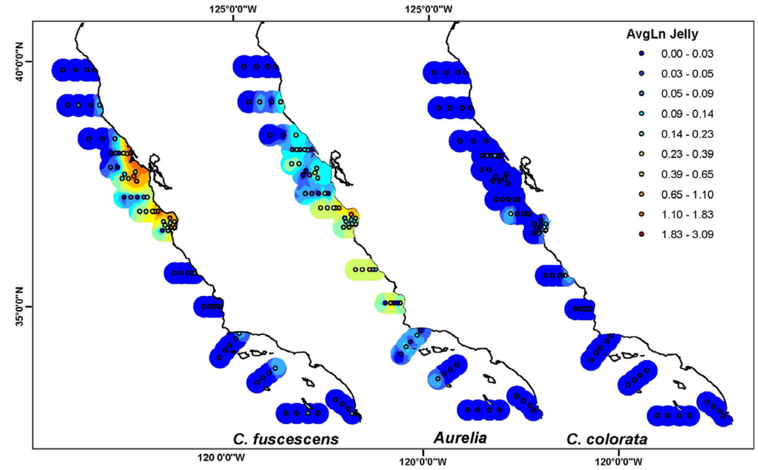


Fig. 4.1.2 Relative abundance (log of the average numbers of individuals per haul) of the three key species of Scyphomedusae, *Chrysaora fuscescens*, *C. colorata* and *Aurelia labiata*, in southern California Current waters in the May–June period, from 2005–2012 (Field, unpubl.).

4.1.3 Long-term changes in relation to environment

Densities of the two dominant larger medusa species, the scyphozoan *Chrysaora fuscescens* and the hydrozoan *Aequorea* spp., have been monitored as part of a pelagic trawl survey in the northern California Current conducted every June and September since 1999 (Suchman *et al*., 2012). With few exceptions, *C. fuscescens* dominated the catch and was generally 1 to 2 orders of magnitude higher than that of *Aequorea* (Fig. 4.1.3). Catches of both species returned to a more typical level in June 2012, following below-average catches for 2010 and 2011, possibly due to the lingering effects of the 2010 El

Niño. In September 2012, catches of both species were similar to 2011, with densities of *C. fuscescens* being approximately an order of magnitude higher than those of *Aequorea*, similar to that seen in earlier years by Suchman *et al*. (2012).

Salps (mostly *Thetys vagina* and *Salpa fusiformis*) have been enumerated from large fine-mesh midwater trawl collections off Oregon and Washington since 2004. Data come from four cross-shelf transects typically sampled from May–September. Catches were very low (zero in many cases) from June 2004 until June 2010 when salp densities increased precipitously reaching a maximum of 3400 individuals 10^6 m^{-3}, which coincided with the 2010 El Niño period (Fig. 4.1.4). Densities continued to be high early in 2011 when they began to taper off and return to near normal low catches in 2012.

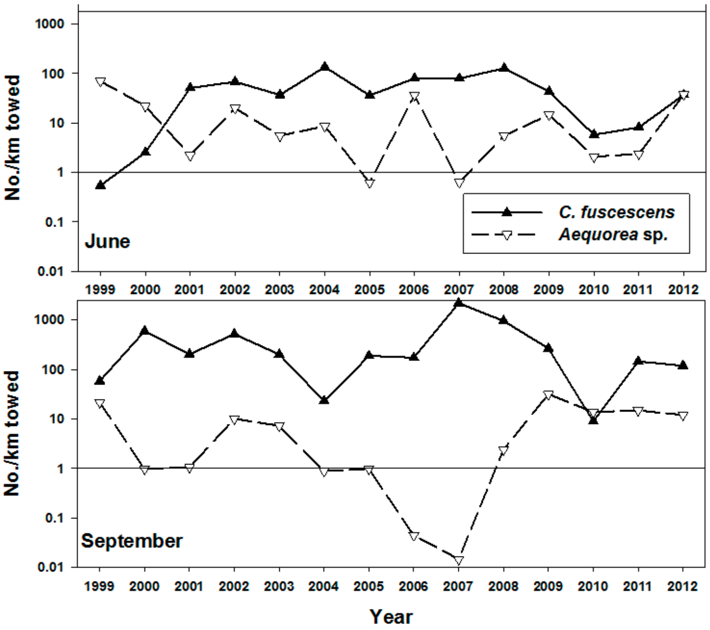


Fig. 4.1.3 Catches of *Chrysaora fuscescens* and *Aequorea* spp. in annual surface trawl surveys off Washington and Oregon in June (top) and September (bottom) from 1999–2012 (from Suchman *et al*., 2012).

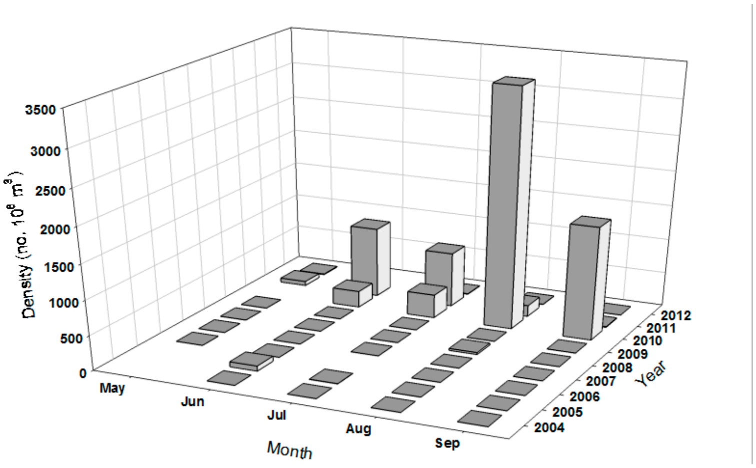


Fig. 4.1.4 Densities of salps collected in fine-mesh midwater trawls by month from 2004–2012 showing the massive bloom that occurred in 2010 and 2011 in the northern California Current (Brodeur, unpubl.).

Another long-term data set involves the by-catch of gelatinous zooplankton (mostly large medusa) in triennial bottom trawl surveys conducted by the Alaska Fisheries Science Center, NOAA from 1980–1992 (data provided by M. Wilkins, AFSC, NOAA) that extend from northern Washington to southern California. Catches were highly variable but showed low jellyfish abundance during the 1983 and 1998 El Niños (Fig. 4.1.5), similar to other studies discussed above, but also in 1986.

With respect to temporal trends in abundance in the southern California Current, the juvenile fish trawl survey data were described in Bjorkstedt *et al.* (2012) who reported the mean log-transformed catch of *C. fuscescens* and *A. labiata* for the core survey area between 1990 and 2012 (excluding the years 2002–2004, for which data were not collected). The index (Fig. 4.1.6) can be used as a relative abundance time series, as Bjorkstedt *et al.* (2012) have not yet developed an absolute abundance index given the uncertainty regarding net selectivity and the real or likely depth stratification of jellyfish, which is likely present at greater densities in the upper 20 m of the water column relative to the 30- to 40-m depths targeted in the trawl survey. Moreover, the catches from the time series only represent catches from non-problem tows in the survey database and consequently exclude information from “problem hauls” in which the nets were either damaged or “blown out” due to extremely high (but subsequently un-quantified) hauls, or in which hauls were aborted due to the high presence of jellyfish in the water.

Although Bjorkstedt *et al.*’s analysis is ongoing in incorporating the information from such problem hauls into a revised jellyfish index, a preliminary analysis suggests that the general trends inferred by the catches are consistent with those that are inferred when the problem hauls and blowouts are similarly included. Thus, Bjorkstedt *et al.*’s index reflects the best available information on relative abundance and trends for these two species in the Central California region. With respect to absolute abundance, some work has been done to develop estimates of jellyfish abundance in this region using acoustic backscatter from which estimates of abundance by area were developed for the Monterey Bay and Gulf of the Farallones regions (Graham *et al.*, 2010), with mean densities estimated to be on the order of a quarter of a million jellyfish within a square mile of ocean habitat. Ultimately, some combination of net sampling and acoustics could lead to greatly improved estimates of abundance, distribution and year-to-year variation in large scyphomedusae in the Central California region.

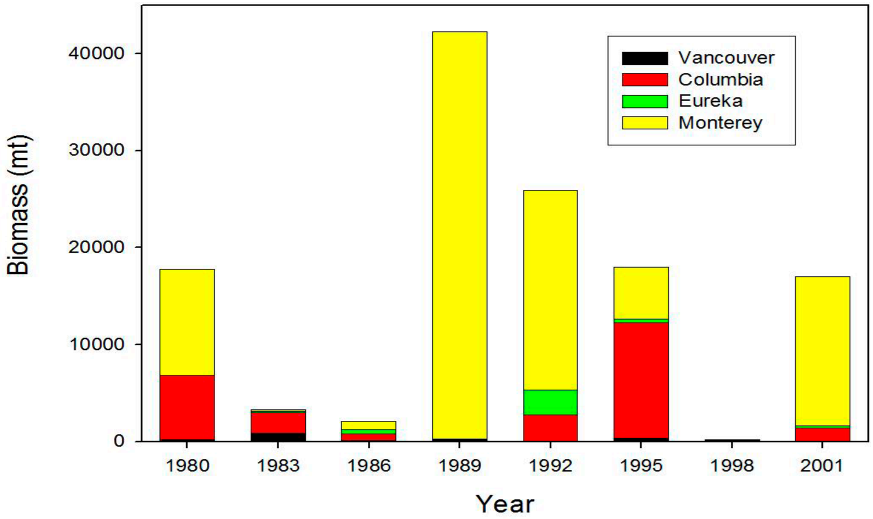


Fig. 4.1.5 Catch of jellyfish (all species combined) from U.S. west coast bottom trawl surveys conducted every three years from 1980–2001 by geographic area (data provided by M. Wilkins, AFSC, Seattle).

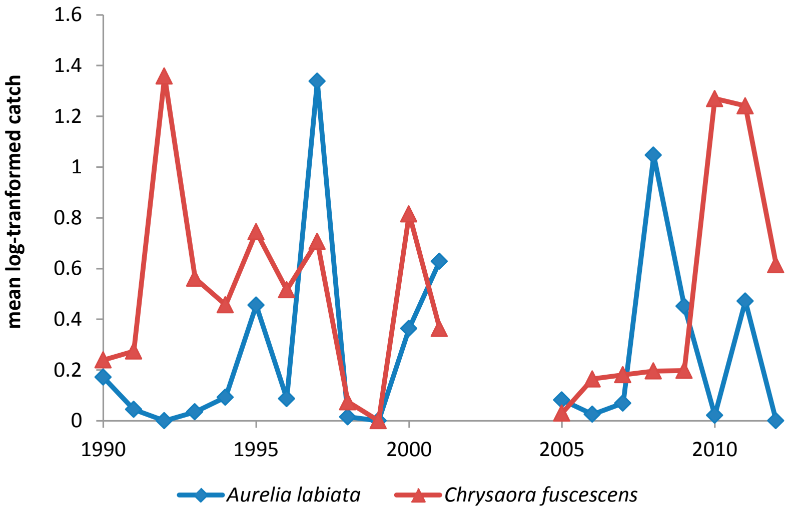


Fig. 4.1.6 The mean of the log-transformed catch rate for the two most frequently occurring scyphozoan species encountered in the Southwest Fisheries Science Center (NMFS, NOAA) midwater trawl survey conducted off Central California from 1990–2012 (from Bjorkstedt *et al*., 2012).

The temporal trends observed in this index suggest both high interannual variability (consistent with high interannual variability observed in many of the time series of micronekton documented in this juvenile fish trawl survey), and no clear indication of either a monotonic increase or decline in jellyfish abundance in the Central California region over time. Previous reviews for this region have noted that blooms have been historically described as frequent events, such as the account of Galigher (1925) who noted "the hordes of jellyfish which appear annually along our shores." In an analysis of temporal covariability with other micronekton collected from the survey (J. Field, unpubl. data, but see Bjorkstedt *et al*., 2012), the years of greatest jellyfish abundance tended to be relatively cool, high transport years that also favored increased abundance of young-of-year groundfish, krill and market squid, while during warm, less productive years (such as the 1998 El Niño year and the unusually low productivity period between 2005–2006), jellyfish abundance declined considerably. Modest, but significant, negative correlations were also found between the abundance of *C. fuscescens* and a lagged Pacific Decadal Oscillation (PDO) index, and between *A. labiata* and the Multivariate ENSO index. However, abundance also appeared to correlate with local variables such as mean chlorophyll levels in near-surface waters, and the mean depth of the pycnocline in nearshore waters. A more comprehensive analysis of the large-scale and regional physical factors that relate to jellyfish abundance and distribution in this region is currently in progress. Off California, the temporal trends of midwater hydromedusae have been related to major climate forcing events such as El Niños (Raskoff, 2001).

4.2 West Coast of Canada

Mary N. Arai[1] and Moira D. Galbraith[2]

[1] Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, British Columbia, Canada
[2] Fisheries and Oceans Canada, Institute of Ocean Sciences, Sidney, British Columbia, Canada

4.2.1 Introduction

Knowledge of jellyfish diversity, abundance, biomass, and distribution along Canada's Pacific coast is relatively poor — they are not commercial species and do not interfere (generally) with human activity along the coast. Nevertheless, populations and other information on smaller jellyfish species (especially Hydromedusae) can be gleaned from extensive zooplankton datasets from a few regions off the west coast of Canada and Washington State in the U.S. Studies beginning in the 1860s have examined a variety of jellyfish species in a number of discrete locations but until fairly recently generally lacked regular long-term monitoring.

The most extensively examined area off the west coast of Canada is the Salish Sea and its adjacent bays, which run primarily north–south. The area includes waters of both Canada and the U.S., such as the Strait of Georgia and Puget Sound which lie just to the west of mainland British Columbia and Washington. They contain lower salinity and higher amounts of sheltered habitat than the outer coast. The fauna of the Salish Sea is described separately in section 4.3.

The remaining Canadian regions (Fig. 4.2.1) include the northern portion of the California Current area comprised mainly of a portion of continental shelf off Vancouver Island; an offshore area of the northern west coast of Vancouver Island, mainland inlets and Queen Charlotte/Hecate Strait up to Dixon Entrance collectively referred to as the Pacific Coast; a survey of Masset Inlet; a western open ocean area of the Gulf of Alaska, and an offshore 1400-km transect known as 'Line P' which extends toward Station Papa (50°N 145°W) in the Alaska Gyre. The latitudinal position of the boundary between the Alaska Current and the California Current is variable, dependent on seasonality and gyre positioning.

One long-term effort from the west coast of Canada is part of a government-sponsored zooplankton monitoring program. Fisheries and Oceans Canada (also known as the Department of Fisheries and Oceans or DFO) has been collecting zooplankton off the British Columbia coast for decades, and amalgamating the zooplankton information into one database (IOS Zooplankton Database; www.dfo-mpo.gc.ca/science/data-donnees/plankton-plancton/basedonnees-zooplankton-database-eng.html). Also, while all these surveys enumerate many smaller coelenterate species, most have intentionally avoided large scyphomedusae and have re-done samples (in the field) that have chance encounters with large jellyfish.

For the time series presented here, most gelatinous zooplankton were aggregated in four major groups and data were calculated as average abundance or annual biomass anomalies (annually averaged log10-scale deviations) as outlined in Mackas *et al*. (2001, 2004). Data on biomass for zooplankton gelatinous groups is presented in graph form. This information is a compilation from the IOS Zooplankton Database and is expressed as an average yearly biomass by area and major groupings.

As part of the La Perouse Bank Monitoring Program of DFO, zooplankton samples were collected on the southern outer coast of British Columbia, along both the continental shelf of Vancouver Island and farther offshore. Typically, samples from the outer coast of Vancouver Island are grouped in two regions: northern Vancouver Island and southern Vancouver Island, with the borderline being just north of Estevan Point. The position of the boundary between consistent sampling methods from these areas allows comparison of data extending back to the late 1970s and early 1980s. The early years are less reliable due to smaller numbers of stations sampled but by the 1990s the monitoring program was fairly well established on all science research vessels. Similar data on lumped "jellyfish" from 1985–1998 are included in Mackas *et al*. (2001).

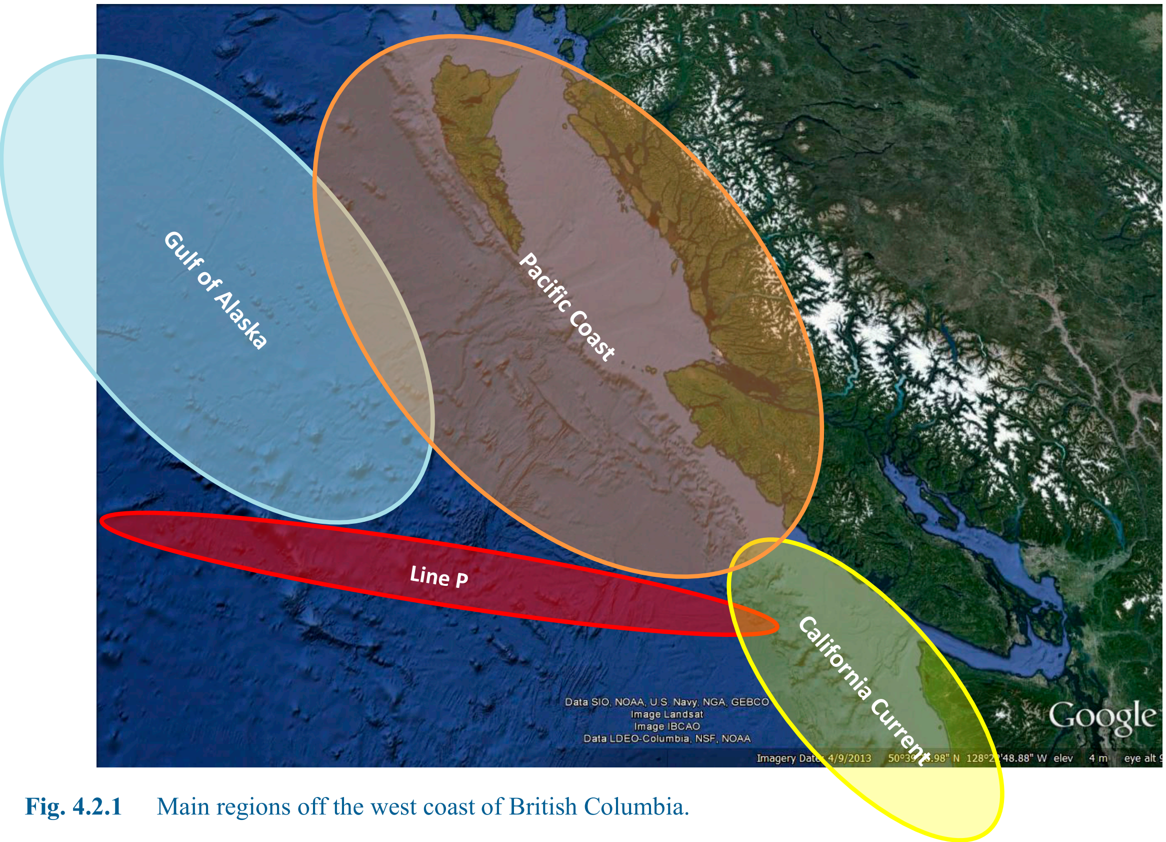


Fig. 4.2.1 Main regions off the west coast of British Columbia.

4.2.2 Hydromedusae

There has been a variety of work on Hydromedusae over the years by various research institutes. Taxonomic work on populations other than in the Salish Sea is included in a monograph (Arai and Brinckmann-Voss, 1980) which was updated in 1998 (Brinckmann-Voss and Arai, 1998). The yearly life cycle, especially of *Sarsia*, was examined in Masset Inlet (Arai, 1987). *Polyorchis penicillatus* is most abundant in the harbors of the outer coast of Vancouver Island and Queen Charlotte Islands (Haida Gwaii) (Arai and Brinckmann-Voss, 1980) where it has been collected for the study of locomotion. The May to August release of *Aglantha*, *Eutonina*, *Solmissus*, *etc*. was examined off the La Perouse area of the west coast of Vancouver Island and at Station P (Arai and Fulton, 1973; Fulton *et al*., 1982; McFarlane *et al*., 1997). The migration and vertical ranges of selected Hydromedusae were quantified off the west coast by Mackie from 1980 to 1983, using a submersible to observe movement (Mackie, 1985).

The majority of hydromedusae caught off the west coast of Vancouver Island by net (Fig. 4.2.2) are *Aglantha, Mitrocoma, Clytia* and *Aequorea*; farther off shore it is mainly *Aglantha*. In recent years, hydromedusae have become more numerous over the shelf area off the west coast, often associated with warm water intrusions from the south (Mackas *et al*., 2001) or with vent fields (Burd and Thomson, 1995).

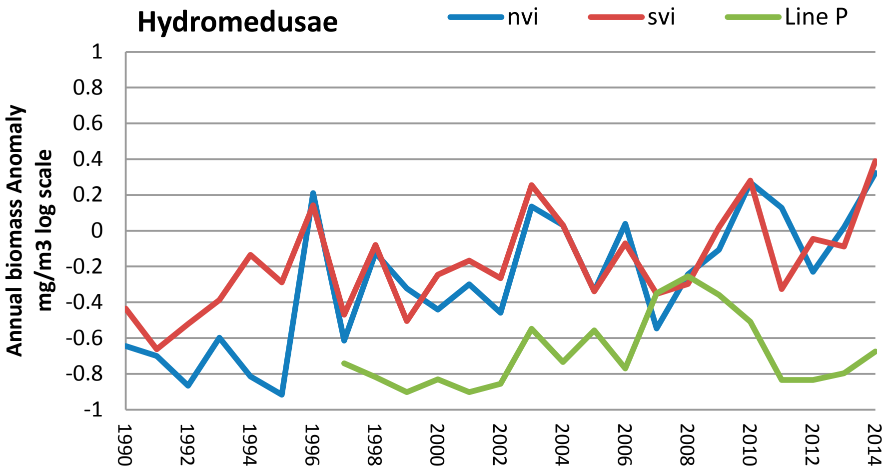


Fig. 4.2.2 Hydromedusae from northern (nvi) and southern (svi) Vancouver Island and Line P. Net samples from the IOS Zooplankton Database (from Galbraith, unpubl.).

In addition to the medusae, hydroid portions of Hydrozoa may be separately present in the water column. In the Pacific, large numbers of sailed hydroid colonies of *Velella* have been found north to the west coasts of Vancouver Island and the Queen Charlotte Islands (Arai and Brinckmann-Voss, 1980). The distribution depends apparently on the extent of the offshore currents. The very small medusae have not yet been collected in this part of the ocean. Although the hydroid colonies have often been observed stranded in large numbers on the beaches, they are seldom collected by routine collections with nets. The presence of *Velella velella* along the west coast of Vancouver Island is used as an indicator of water being propagated shoreward as opposed to poleward (Table 4.2.1).

Table 4.2.1 *Velella velella* collected from vertical net samples from 1970–2014 off the west coast of British Columbia, positive samples only (from Galbraith, unpubl.).

Biomass (mg m^{-3})	1977	1981	1983	1997	2000	2003	2004	2005	2006	2011	2013	2014
Line P	7.3	–	–	44.8	13.4	2.7	9.1	–	–	–	–	–
Northern Vancouver Island	–	–	–	–	–	–	–	107.4	69.3	144.8	129.7	248.9
Southern Vancouver Island	–	6.9	1.3	–	–	–	–	179.3	2482.7	–	506.3	34.6

4.2.3 Siphonophora

The taxonomy and biology of siphonophores in Canadian Pacific waters have been described in a monograph by Mapstone (2009) with a section on ecology by Arai (2009). Although 37 species of siphonophores were identified in this area, presence in the upper 100 m is largely restricted to the neritic codonophore *Muggiaea atlantica*. Off the west coast of Vancouver Island (Fig. 4.2.3) the codonophores *Dimophyes arctica* and *Lensia conoidea*, and the physonect *Nanomia bijuga* were most abundant in the upper 700 m (Mackie, 1985; Mapstone, 2009). Occasionally, individual bracts and nectophores from large physonect siphonophores are caught in net samples making it difficult to determine species but the large colonial forms of *Praya* and *Bargmannia* have been observed from submersibles.

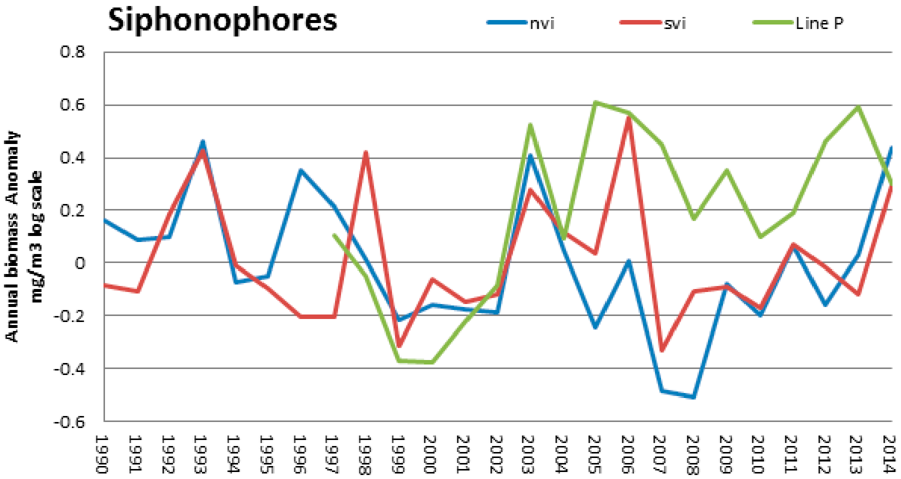


Fig. 4.2.3 Siphonophores from northern (nvi) and southern (svi) Vancouver Island and Line P. Net samples from the IOS Zooplankton Database (from Galbraith, unpubl.).

4.2.4 Scyphomedusae

Data on Scyphomedusae are now being collected by DFO's integrated ecosystem surveys. These surveys are conducted several times each year, often with a focus on juvenile salmon. 'Inshore' surveys are conducted in the Strait of Georgia (Salish Sea) and surrounding inlets as part of the Georgia Strait Trawl Survey. Similar 'offshore' surveys are also conducted around Vancouver Island (in inlets and offshore), as well as farther north along the Pacific coast of British Columbia as part of the High Seas Salmon Survey. These surveys are fish-directed but Scyphomedusae are counted and weighed as part of by-catch. In the past, the medusae would have been ignored and discarded. Surveys are conducted along repeated transects three times a year and therefore, are useful for identifying both seasonal and interannual trends. The survey programs use similar fishing gear, namely, a midwater trawl net with an approximate mouth opening of 28 m wide by 16 m deep (Trudel *et al*., 2010). Typical trawls are fished at the surface or at a measured depth for 30 minutes at 5 knots. While the trawl may inflict significant damage to the jellyfish in the catch, medusae are often intact and identifiable to species. These trawls frequently catch large scyphomedusae such as *Chrysaora fuscescens, Aurelia labiata*, *Cyanea capillata*, and *Phacellophora camtschatica*. Smaller species, Hydromedusae *Aequorea*, ctenophores and siphonophores colonies, are also captured when abundant (Fig. 4.2.4).

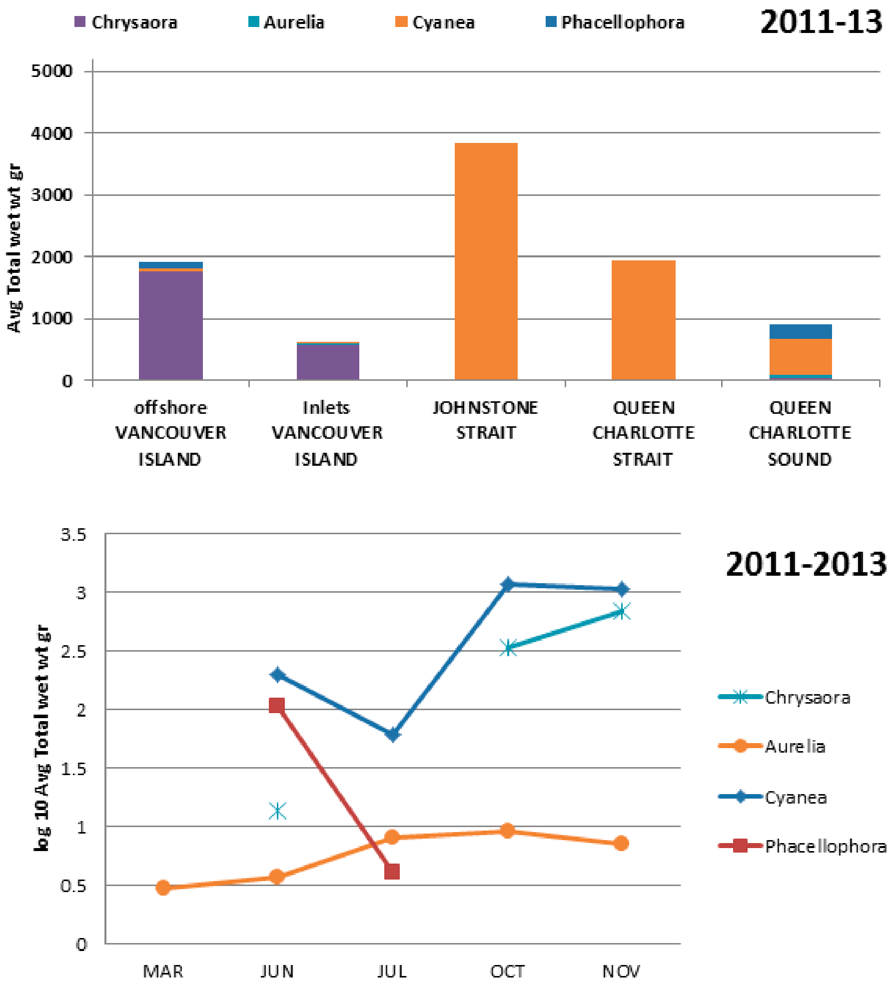


Fig. 4.2.4 Preliminary results from survey transects, High Seas Salmon Surveys, west coast of British Columbia, November 2011 to March 2013. Top panel by area; lower panel by month (from M. Trudel, DFO, unpubl.).

Since 2011 these surveys have been enumerating jellyfish abundance and biomass, and it is hoped that the results will provide a better understanding of jellyfish diversity and distribution in B.C. coastal waters, along with the identification of seasonal and interannual trends in abundance and biomass. In this preliminary dataset, the stations in the Strait of Georgia had little to no capture of scyphomedusae but what was entrained in the trawls was mainly *Cyanea.* Not all the data were available at the time of this Working Group report.

During ichthyoplankton surveys off the west coast during the early 1980s, two genera of Scyphomedusae, *Atolla* and *Periphylla*, were observed in the deep-water canyon areas along the transects (Fulton *et al.*, 1982). Bathypelagic species of Hydromedusae are poorly understood or even documented and are only now being investigated with the development of remotely operated deep-water multi-net samplers.

4.2.5 Ctenophora

The majority of ctenophores captured by net off the west coast of British Columbia (Fig. 4.2.5) are *Pleurobrachia*. In areas where net sampling goes below 150 m *Beroe* is also captured, usually singularly, whereas *Pleurobrachia* is often found in dense patches in the upper 50 m. Many of the more delicate species, such as *Bolinopsis* sp., are often destroyed by the sampling method and therefore, underrepresented in the tabulated results. Periodically, fall and winter currents (or El Niño events) bring small patches of *Horminophora* and *Thalassocalyce* onto the southern Vancouver Island shelf from California/Oregon.

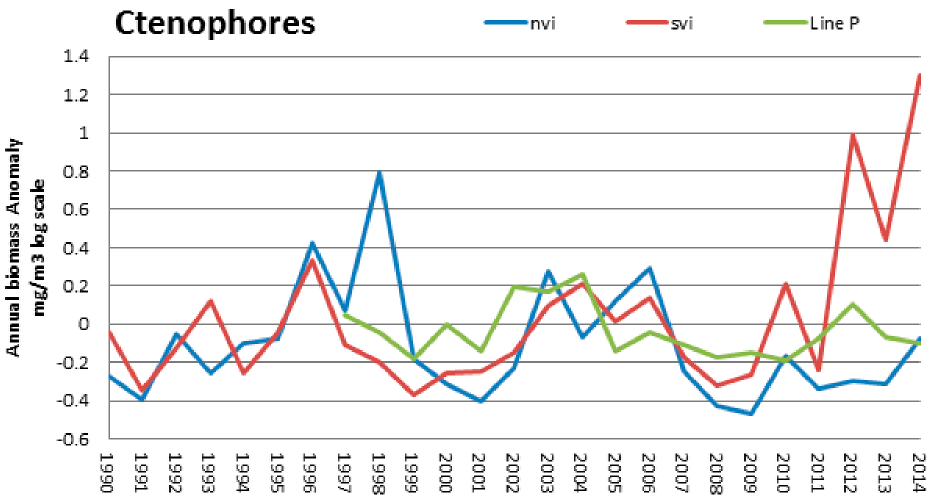


Fig. 4.2.5 Ctenophores from northern (nvi) and southern (svi) Vancouver Island and Line P. Net samples from the IOS Zooplankton Database (from Galbraith, unpubl.).

4.3 Salish Sea

Moira D. Galbraith[1], Jennifer Purcell[2], Richard Brodeur[3] and Mary N. Arai[4]

[1] Fisheries and Oceans Canada, Institute of Ocean Sciences, Sidney, British Columbia, Canada
[2] Shannon Point Marine Center, Western Washington University, Anacortes, Washington, USA
[3] Northwest Fisheries Science Center, Hatfield Marine Science Center, National Marine Fisheries Service, NOAA, Newport, Oregon, USA
[4] Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, British Columbia, Canada

4.3.1 Introduction

The Salish Sea includes both Canadian and U.S. waters. In Canada, the Strait of Georgia runs from Johnstone Strait southeast past the cities of Nanaimo and Vancouver and the mouth of the Fraser River to the Canada–U.S. boundary at the Gulf Islands and San Juan Islands. The Strait of Georgia is bordered to the east by mainland British Columbia and to the west by Vancouver Island (Fig. 4.3.1). Mean and maximum depths of the Strait of Georgia extend 155 and 420 m, respectively (Thomson, 2014). From the south end of the Strait of Georgia, Juan de Fuca Strait connects westward to the open Pacific whereas Puget Sound, including the Hood Canal, extends south past the cities of Seattle and Tacoma. Bodies of water attached to the Strait of Georgia vary greatly in length and depth from Roscoe Bay in the north running only approximately 1 km into West Redonda Island to fjords such as the southern 22 km long Saanich Inlet.

The lower salinity and high proportion of sheltered habitat of the Salish Sea and adjacent bays has attracted both field- and laboratory-oriented researchers to a number of areas of this sea for many years, making it comparatively convenient to survey, examine and analyze the zooplankton populations separately from those of the outer coast. Much of the earliest taxonomic and experimental works were carried out in the summer season by academic scientists.

The first annual zooplankton time series of Fisheries and Oceans Canada (also known as the Department of Fisheries and Oceans (DFO)) has been concentrated on analysis of sampling data of the last 50 years from the central Strait of Georgia (Mackas *et al*., 2013). In spite of the fragility of gelatinous specimens, gaps and storage problems due to the large size of various scyphozoan medusae, and irregular sampling, it has been established that the summer and autumn group of ctenophores and medusae is more abundant than any other group except for the spring and summer copepods.

DFO has been collecting zooplankton samples in a variety of locations in the Strait of Georgia since 1950, but only recently has been using consistent methods. The anomaly analysis is therefore, restricted to samples taken using a vertical net haul, using either a SCOR, Bongo or NorPac net, and samples the full water column (5 m off the bottom to surface; see Mackas *et al.* (2013) for full explanation of the methods). Examining the time series anomalies for three of the gelatinous zooplankton groups (hydromedusae, siphonophores and ctenophores), there are large interannual and decadal variations but no consistent trends over the last 22 years (Fig. 4.3.2). There was a positive change in the years following the 1997 El Niño event, with a bumpy decrease of all three groups from the 2000s to 2008. All three groups showed a positive anomaly in 2011, and hydromedusae and siphonophores remained higher than average in the subsequent two years (Fig. 4.3.2).

Fig. 4.3.1 The Salish Sea which is bounded by Discovery Islands to the north, British Columbia/Washington to the east, mouth of Juan de Fuca Strait to the west, and the southern extent of Puget Sound.

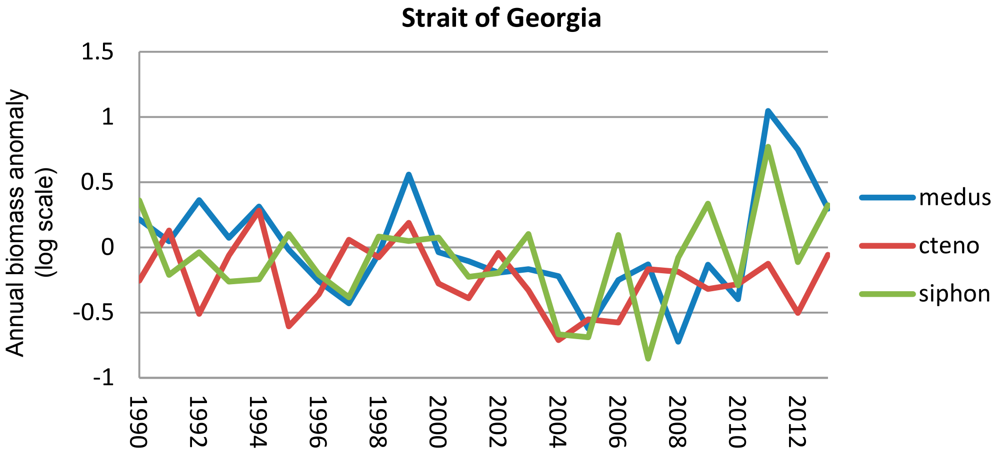


Fig. 4.3.2 Gelatinous zooplankton anomalies in the Strait of Georgia, including hydromedusae (medus), ctenophores (cteno), and siphonophores (siphon) (from Galbraith, unpubl.).

4.3.2 Hydromedusae

Hydrozoa were among the first groups of planktonic animals to be collected and described on the west coast of Canada (Foerster, 1923; Arai, 1992). The earliest recorded collections of hydromedusae were made by A. Agassiz in 1862 in the Strait of Georgia. C. McLean Fraser, a distinguished hydroid taxonomist, became a curator at the Pacific Biological Station in Nanaimo and later a professor at the University of British Columbia, Vancouver. His Masters' student, R. E. Foerster, examined live and preserved hydromedusae collected mostly at the Pacific Biological Station from 1912–1921 (Arai, 2004). A description of further hydromedusan taxonomy and distribution in the Salish Sea (including both the Strait of Georgia and Puget Sound) was summarized in a 1980 monograph (Arai and Brinckmann-Voss, 1980) and updated in 1998 (Brinckmann-Voss and Arai, 1998).

Most studies in both countries generally have lacked continuous long-term monitoring. Nevertheless, the ecology of the hydromedusae is better known in the Salish Sea than anywhere else in the world. The vertical distribution and behavior of *Aglantha digitale* in Saanich Inlet in 1965 was examined by Arai and Fulton (1973); Arai and Mason (1982) examined data on the abundance and depth of holoplanktonic *A. digitale* and *Aegina citrea* in Saanich Inlet and in the central Strait of Georgia in spring and summer of 1979 and Mackie (1985) examined several locations in 1981–1983. Mills (1981a,b, 1982, 1983) examined behavior as well as seasonal patterns of occurrence. Larson (1985, 1986a,b, 1987) provided seasonal data on the densities and biomass of the common species of Hydromedusae in Saanich Inlet in 1980–1981 as well as information on feeding and egg production. Purcell (1989, 1990, 1991) and Purcell and Grover (1990) presented data on hydromedusae and zooplankton during the spring hatching of herring larvae from 1983–1987 in a bay on Vancouver Island, as well as predation rates of *Aequorea victoria*, which was shown to be an important predator of herring larvae. The 5-year time series showed extreme interannual variation, with densities varying by up to three orders of magnitude between years, and predation impact ranging from almost none to all of the herring larvae annually (Purcell and Arai, 2001). Mean jellyfish densities during the 5 years showed a significant positive correlation with both temperature and salinity (Purcell, 2005). *Aequorea victoria* is also an important predator of other species of Hydromedusae (Purcell, 1991). Purcell and Mills (1988) concluded, by comparing the diets and nematocysts of pelagic hydrozoans, that two groups existed: those that eat mainly prey with exoskeletons, such as crustaceans, and those that eat mainly soft-bodied prey, including fish eggs and larvae, and other jellies. The first group included Anthomedusae (Family Pandeidae), Limnomedusae and Trachymedusae which have nematocysts that can adhere to prey; the second group included Anthomedusae, Pandeidae, Leptomedusae and Narcomedusae, which lacked adhering nematocysts. Later, Costello and Colin (2002) and Colin *et al*. (2003) found different behaviors and similar differences in diet among Hydromedusae.

Although *A. digitale* is the most abundant medium-sized species, the more extensively examined hydromedusae of the Salish Sea are *Gonionemus* sp. and *Aequorea* sp. due to their greater size compared to most Hydromedusae species (Edwards, 1976; Reum *et al*., 2010). *Gonionemus* was an early study of a probable introduction of medusae due to the commercial movement of hydroid-bearing oysters (Edwards, 1976). *Aequorea* was sampled in the spring over a 5-year period in two locations (Kulleet Bay and Baynes Sound on the eastern side of Vancouver Island) in the Strait of Georgia in the mid-1980s, and jellyfish densities were calculated for each year (Purcell and Arai, 2001). The data again, suggest extreme interannual variation, with densities varying by up to three orders of magnitude from one year to the next. Physical data are also available from one of the sampling sites, with mean jellyfish densities showing a significant positive correlation with both temperature and salinity (Purcell, 2005). *Clytia* and *Obelia* are two examples of very abundant, but tiny and little examined, medusae and hydroids. The general trends in biomass of hydromedusae in the Strait of Georgia show recent high values but no long-term trends (Fig. 4.3.3).

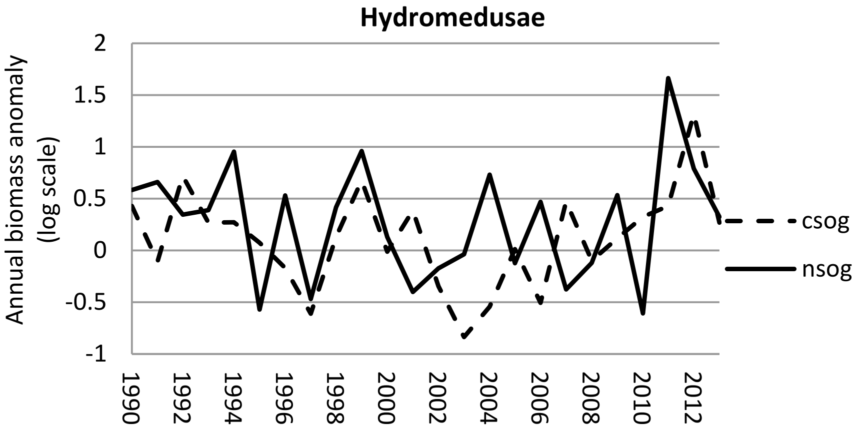


Fig. 4.3.3 Variation in Hydromedusae biomass, comparing the northern Strait of Georgia (nsog) to the central Strait of Georgia (csog) (from Galbraith, unpubl.).

4.3.3 Siphonophora

Colonial siphonophores are widely present in the Salish Sea where they have been observed from a submarine (Mackie, 1985). The predominant species inshore (Purcell, 1989, 1990) and best documented neritic condonophoran siphonophore worldwide (Mackie *et al.*, 1987) is the diphyid calycophoran *Muggiaea atlantica.* Found mainly in the upper 100 m of temperate and subtropical coastal waters, it was the principle siphonophore in Friday Harbor from 1976–1980 (Mills, 1981a; Purcell, 1982) and in Saanich Inlet during 1980–1981 (Mackie and Mills, 1983; Larson, 1986b). Purcell (1982) reported on densities and feeding effects of *M. atlantica*, which is the only existing study on its ecology to our knowledge.

In the central Strait of Georgia and its various deep fjords, the most abundant siphonophores are *Dimophyes arctica* and *Nanomia bijuga* (Mackie, 1985; Mapstone and Arai, 1992). *Dimophyes arctica* was the dominant species in the central Strait of Georgia in samples taken in the spring/summer of 1979, with a maximum density of 4.8 anterior nectophores per cubic meter (Mapstone and Arai, 1992). *Cordagalma cordiformis* was also observed. Distributions and ecology of these species and the more controversial taxonomy of possible *Lensia* sp. are discussed in detail in the monograph by Mapstone (2009). Siphonophores have shown generally higher abundances since 2011 (Fig. 4.3.4).

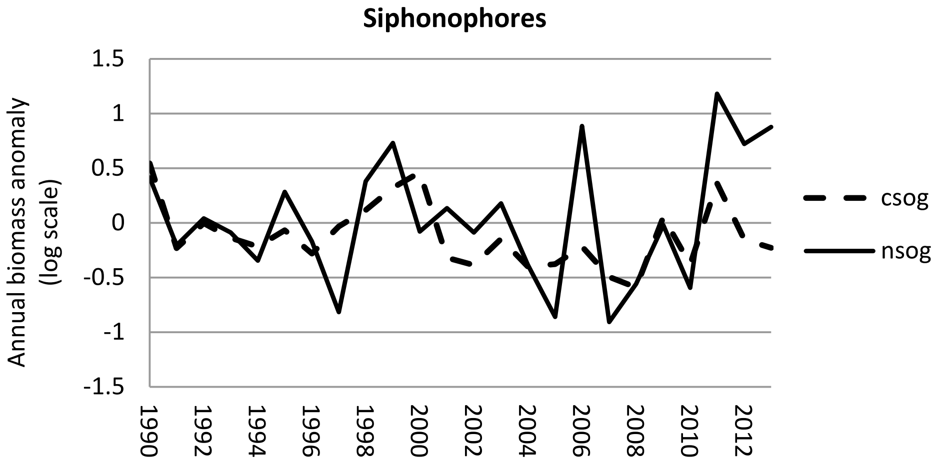


Fig. 4.3.4 Variation in siphonophore biomass in the northern (nsog) and central (csog) Strait of Georgia (from Galbraith, unpubl.).

4.3.4 Scyphomedusae

Three species of these large medusae are common in the Salish Sea: *Aurelia labiata, Cyanea capillata* and *Phacellophora camtschatica.* Polyps of *A. labiata* release ephyrae into the bays of southern British Columbia and northern Washington State at rates affected by temperature, salinity and light (Purcell, 2007; Purcell *et al*., 2009; Reum *et al*., 2010). In Saanich Inlet and in the Hood Canal (Puget Sound), *Phacellophora* and *Cyanea* are the prime predators of *Aurelia* (Strand and Hamner, 1988). They utilize active diel vertical migrations in contacting their prey (Moriarty *et al*., 2012).

Experimental work on some aspects of the physiology and ecology of *A. labiata* (previously confused with *A. aurita* s.l.) is discussed in section 5. However, the movements of the medusae are also of interest. *Aurelia* is able to use a "sun compass" to migrate in a southeasterly direction along Saanich Inlet during a sunny day and aggregate for spawning. (Hamner *et al*., 1994; Hamner, 1995). Most of the medusae remain within the top 2 m of the water column. The mechanism of this migration behavior is not known.

Formations of *A. labiata* aggregations are advantageous even when spawning is not occurring. Dense aggregations make predation by *Phacellophora* and *Cyanea* more difficult (Purcell *et al*., 2000). They also decrease the loss of individuals from small bays during tidal cycles. Albert (2005) found that the timing of the reproductive cycle in Roscoe Bay (north end of the Strait of Georgia) was very similar to that in Saanich Inlet even though Roscoe Bay is much smaller. Albert (2007) then found that *Aurelia* medusae drifted out of Roscoe Bay on turbulent ebb tides and swam down to enter counter current relatively still layers of water beneath the ebb stream. At the turn of the ebb tide these medusae then rose into the relatively still layers of water of the inward flood stream and were returned to the bay. They were not stranded by low ebb tides (Albert, 2008, 2009). As with the "sun compass", the mechanism stimulating this migration behavior is not known (Albert, 2008, 2010) but their behavior indicates that complex neural circuitry is present which can specify the chosen responses elicited by simultaneous incompatible stimuli (Albert, 2014).

Data from Puget Sound show that jellyfish are a major portion of pelagic biomass, and that spatial heterogeneity exists in the relative abundance of jellyfish and small pelagic fishes (Rice *et al*., 2012), and in the species composition of jellyfish assemblages (Reum *et al*., 2010). Based on trawl surveys in inlets inside Puget Sound in June and September 2007, Reum *et al*. (2009) determined that three species of Scyphomedusae (*P. camtschatica*, *C. capillata*, and *A. labiata*) and one species of Hydromedusae (*A. victoria*) were the most common species caught in these waters. The biomass of all species decreased seasonally between June and September for all species, and also showed much variability among the four sampling areas. Rice *et al*. (2012) sampled a broader region of Puget Sound using pelagic trawls from May to August of 2003. Jellyfish from those surveys were not identified to species level but were combined as jellyfish biomass to compare with various fish species that were caught. However, these authors noted that the above species tended to dominate the catch along with the hydrozoan *Mitrocoma cellularia* and ctenophores (primarily *Pleurobrachia bachei*). Jellyfish biomass was highest in the southern part of Puget Sound, often exceeding 80% of the total biomass of the catch, but this decreased substantially northward. Monthly changes were also observed and related to the changing physical environment in the area throughout the summer.

In a recent study, Greene *et al*. (2015) analyzed longer-term patterns of jellyfish biomass using the above studies and comparing them to earlier work done in the 1970s and 1980s. They found that the proportion of hauls with large jellyfish catches increased over this period in all three sub-basins examined, and these were related to increases in anthropogenic stressors, although negatively related to total forage fish biomass. These patterns suggest significant differences in the structure of pelagic food webs within Puget Sound that could have important management implications.

4.3.5 Ctenophora

Ctenophores, or comb jellies, are extremely fragile and most species are not retained in standard sampling or preservation procedures. The majority of the ctenophores remaining in the samples are composed of two species: *Bolinopsis infundibulum* and *Pleurobrachia bachei*. Ctenophores have shown no consistent trends in biomass although in recent years, the northern and southern regions of the Strait of Georgia appear to be out of phase from one another (Fig. 4.3.5). *Bolinopsis infundibulum*, which disintegrates in standard sampling and preservation, occurs in the spring in the Salish Sea (Purcell, 1989, 1990, 1991). *Pleurobrachia bachei* can occur throughout the year, but peaks in spring through summer (Purcell, unpubl.).

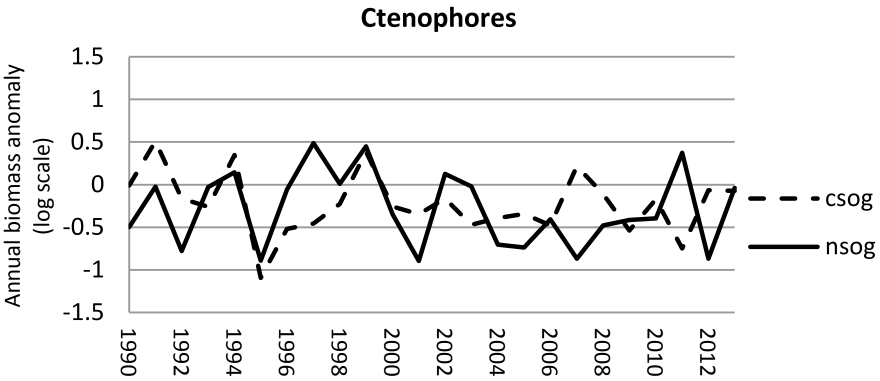


Fig. 4.3.5 Variation in ctenophore biomass in the northern (nsog) and central (csog) Strait of Georgia (from Galbraith, unpubl.).

4.4 Gulf of Alaska

Kristin Cieciel[1] and Jennifer Purcell[2]

[1] Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, Juneau, Alaska, USA
[2] Shannon Point Marine Center, Western Washington University, Anacortes, Washington, USA

4.4.1 Introduction

The Gulf of Alaska (GOA) extends from the eastern Aleutian Islands at 170°W to the Dixon Entrance at 132°40′W, stopping at the Canadian border. It is characterized as a downwelling system that is considered a high nutrient, low chlorophyll environment (Ladd *et al*., 2005) which receives a significant amount of coastal freshwater input and strong winds (Weingartner, 2007). Geographically, it features a narrow continental shelf, glaciers, fjords, and a mountainous coast (Weingartner *et al*., 2009). The GOA's shelf ranges from 5 to 200 km wide, with depths up to 7000 m and covers an area of approximately 370,000 km^2 (Mundy *et al*., 2010). These inputs along with its physical features influence the local meteorology and oceanography creating a diverse marine biological habitat (Weingartner *et al*., 2009).

Jellyfish research in the GOA has been extremely limited in scope and geographic region. A small number of studies have been conducted on specific species but all were limited to a single location, Prince William Sound, Alaska (Fig. 4.4.1; Purcell *et al*., 2000; Purcell and Stardevant, 2001; Purcell, 2003). In addition, very few large-scale GOA research projects have published data on annual jellyfish bloom conditions or biomass and abundance. A recent effort combining data from multiple surveys has documented an unusually large bloom of salps (mainly *Salpa aspera* and *Cyclosalpa bakeri*) along the margins of the GOA during the spring through fall of 2011 (Li *et al*., 2016).

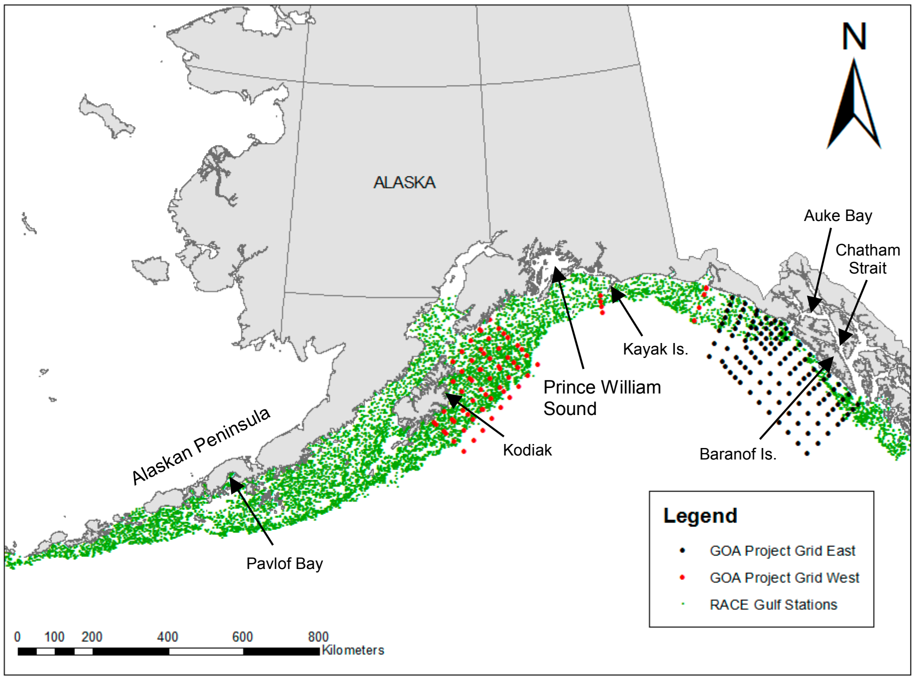


Fig. 4.4.1 Station map for the three current long-term monitoring projects in the Gulf of Alaska. These are typical station grids, which may vary between years due to weather and other factors.

Large-scale monitoring projects in the GOA have now begun to include jellyfish in their research objectives (Fig. 4.4.1). Each of these studies has a different primary research focus but all of these encounter jellyfish as by-catch and record the information. The three interdisciplinary surveys, when combined in terms of spatial and temporal scope with the addition of the Prince William Sound work by Purcell *et al*. (2000) and a historical shrimp trawl study, appear to be comprehensive in coverage area. However, due to inconsistencies in methods, generalized identifications and short or inconsistent time series, the information available is limited and should be used conservatively.

4.4.2 Gulf of Alaska Project

The GOA Project coordinates annual fisheries and oceanographic studies using a series of surface trawls, oceanographic instrumentation, and zooplankton net tows to investigate ecological conditions and juvenile forage fish in the eastern GOA. It is an integrative ecosystem approach to understanding the first year of life of five species of groundfish that are economically and ecologically important. It specifically targets commercially important young-of-the-year groundfish and juvenile salmonid species during July–August in federal waters up to 100 miles offshore from the south end of Baranof Island to Kayak Island, Alaska. After jellyfish were observed in notable numbers in the surface trawl catches, protocols were modified in 2011 to include detailing their presence in the catch (Fig. 4.4.2).

Stations are located every 50 km along each transect. At each station fish and invertebrates are collected using a 198-m long midwater rope trawl with hexagonal mesh wings and body and a 1.2-cm mesh liner in the codend. The rope trawl is towed at 3.3–7.0 km hr^{-1} at an average of 5.6 km hr^{-1} at or near the surface, and has an average horizontal spread of 40.3 m and an average vertical spread of 36.0 m. All tows last 30 minutes and cover a distance of 1.7–3.5 km. The surface trawl catch is sorted to species, with the first 50 jellyfish of each species individually weighed and measured (bell diameter), and combined with the remaining jellyfish for a total weight.

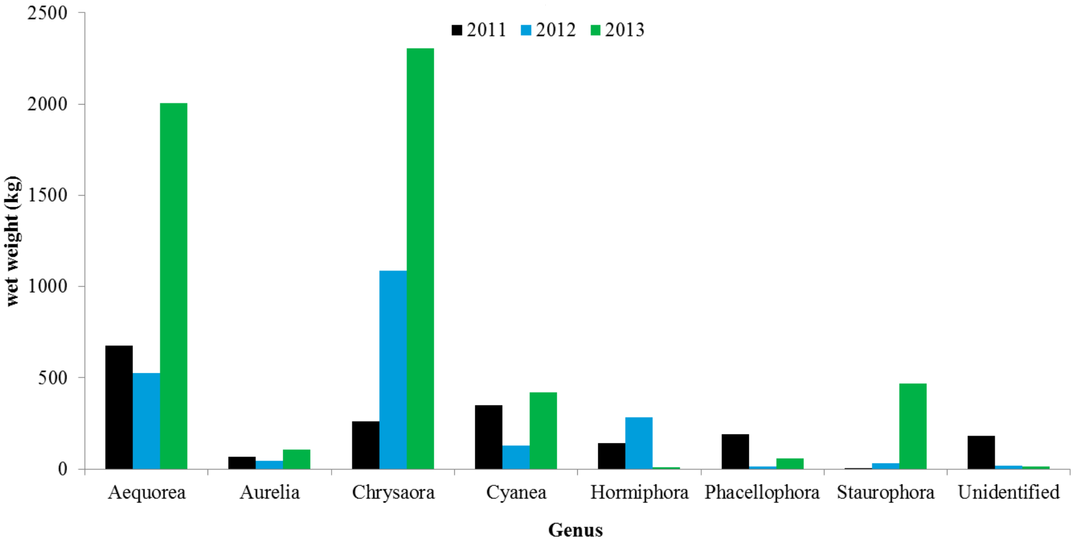


Fig. 4.4.2 Jellyfish composition for the Gulf of Alaska Project, by genus. Catch is wet weight (kg) (from Cieciel, unpubl.).

4.4.3 Southeast Coastal Monitoring survey

The Southeast Coastal Monitoring (SECM) survey began in 1997, typically occurring for one week per month from June–August (Fig. 4.4.3). The survey is conducted in the northern region of southeastern Alaska in an area termed the "Inside Waters" at eight stations in Icy and Chatham Strait with additional zooplankton sampling in Auke Bay. The SECM survey utilizes a Nordic 264 rope trawl fished at the surface (184 m long, mouth opening ~30 m width by 24 m depth) for 20 min at about 1.5 m s^{-1} and covers eight stations per month per region (up to 26 total hauls). Jellyfish are separated from fish catch, identified to genus, counted, and volumetrically measured to the nearest 0.1 liter (L) as a biomass proxy. Zooplankton samples are taken from a vertical plankton tow with conical nets, identified and enumerated to species when possible.

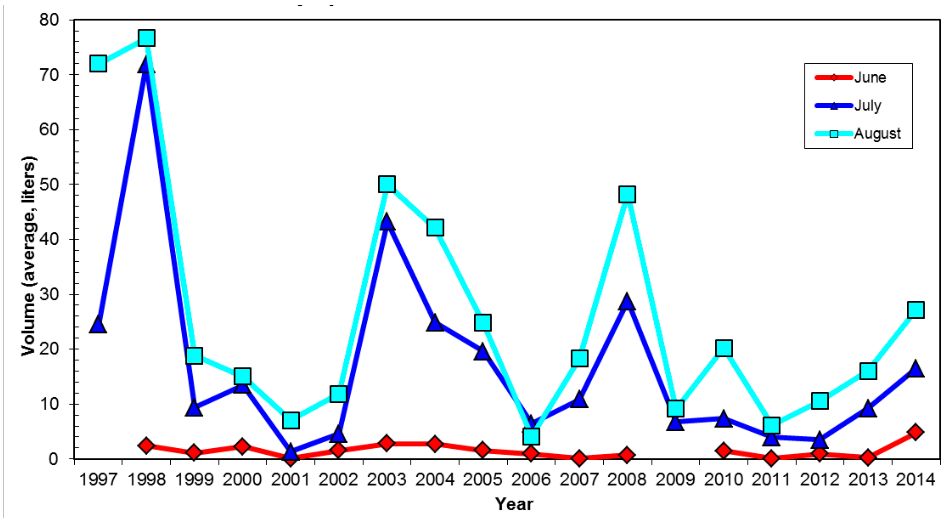


Fig. 4.4.3 Combined jellyfish volume from 1997 to 2014 for the northern region of southeastern Alaska (from Cieciel, unpubl.).

4.4.4 Resource Assessment and Conservation Engineering surveys

The Resource Assessment and Conservation Engineering (RACE) bottom trawl surveys in the GOA are designed primarily to assess populations of commercially important fish and invertebrates. They typically occur May through July. Non-target species, such as jellyfish, are also encountered and are identified, weighed and counted during the course of the surveys, providing a possible measure of relative abundance. Many of the jellyfish species are not sampled well by the gear, or occur in areas that are not well sampled by the survey (hard, rough areas, mid-water, *etc*.) and are therefore, encountered in small numbers which may or may not reflect their true abundance in the GOA. The fishing gear used aboard the Japanese vessels that participated in all GOA surveys prior to 1990 was very different from the gear used by all vessels since. This gear difference almost certainly affected the catch rates. For each species group, the catches for each year were scaled to the largest catch over the time series (which was arbitrarily scaled to a value of 100). The standard error was weighted proportionally to the catch per unit effort (CPUE) to get a relative standard error. The percentage of positive catches in the survey bottom trawl hauls was also calculated. Jellyfish sampling began in 1984 (Fig. 4.4.4).

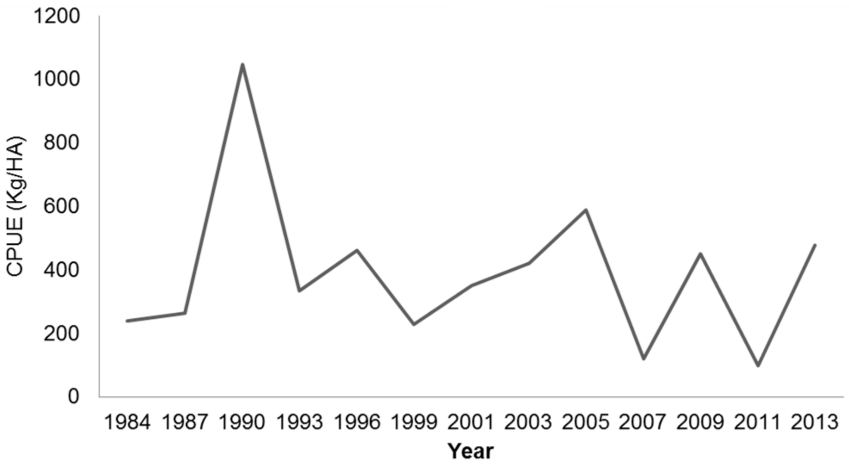


Fig. 4.4.4 Biennial RACE Gulf of Alaska jellyfish bottom trawl survey showing trends in jellyfish bycatch, catch per unit effort (CPUE; kg ha^{-1}). All gelatinous species were pooled as jellyfish (from Cieciel, unpubl.).

The jellyfish mean CPUE is typically higher in the central and eastern GOA than in other areas. The frequency of occurrence in trawl catches is generally high across all areas, but has been variable. Jellyfish catches in the western GOA have been uniformly low. GOA survey results provide limited information about abundance or abundance trends for jellyfish due to problems in catchability. Therefore, the indices presented are likely of limited value to fisheries management.

4.4.5 Shrimp trawl surveys

In 1953–1997, small-mesh trawl surveys for shrimp were conducted by the National Marine Fisheries Service and the Alaska Department of Fish and Game between May and October in the western GOA. These surveys provided by-catch data on jellyfish in the coastal GOA in areas around Prince William Sound, Kodiak, the Alaskan Peninsula, and Pavlof Bay (Anderson and Piatt, 1999). The by-catch was not speciated or measured beyond total weights; all data was lumped general “jellyfish” category. The surveys compared catch data which included jellyfish and climate indices, showing an increase in the jellyfish catches beginning in 1977 with another distinct increase recorded in the late 1980s (Anderson and Piatt, 1999; Purcell, 2005).

4.5 *Bering Sea*

Richard Brodeur[1], Kristin Cieciel[2] and Alexander Zavolokin[3]

[1] Northwest Fisheries Science Center, Hatfield Marine Science Center, National Marine Fisheries Service, NOAA, Newport, Oregon, USA
[2] Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, Juneau, Alaska, USA
[3] Pacific Scientific and Research Fisheries Center (TINRO-Center), Vladivostok, Russia

The following report has been adapted from Decker *et al*. (2014).

4.5.1 Introduction

The Bering Sea lies between 52° and 66°N and 162°E and 157°W (see Fig. 4.5.1). It is bounded by the Bering Strait to the north, the Aleutian Islands to the south and the Alaskan and Russian coasts to the east and west, respectively. The eastern Bering Sea features a broad (~500 km wide) shelf of <200 m depth extending northwestward from the Alaska Peninsula to the eastern tip of the Russian Far East. Sea ice covers the eastern Bering Sea shelf each winter, but the variability in sea ice extent among years is large (*e.g*., Niebauer, 1983) because the region can be dominated by air masses of either maritime or arctic origin (Rodionov *et al*., 2007). The maximum ice extent and timing of the ice retreat in spring represent the primary factors controlling physical conditions on the Bering Sea shelf throughout the year (Stabeno *et al*., 2001, 2012). Seasonal ice cover is also major driver of Bering Sea ecology (Hunt *et al*., 2011). However, summer weather conditions, *e.g*., storminess/wind mixing and amount of insolation can also be important to the water properties (Bond and Overland, 2005) and production (Napp and Hunt, 2001). The physical conditions of the western Bering Sea also show similar biophysical regions in the eastern Bering Sea (Khen, 1999) but the general oceanography of this narrow shelf region is dominated by the Kamchatka Current and its meanderings (Hunt *et al*., 2010).

The eastern Bering Sea is a productive and economically valuable ecosystem supporting rich populations of zooplankton, forage fish, groundfish, crabs, marine birds and mammals. Alaskan commercial fisheries are among the largest in the world, with combined annual landings of nearly 2 million metric tons valued at 1.6 billion USD (NMFS, 2010). The primary fisheries are for groundfish (walleye pollock, flatfish, and Pacific cod), crabs (tanner and king), but some fisheries also exist for salmon and herring and other pelagic fishes. Landing data are less complete for the western Bering Sea but in recent years these have averaged by weight to only be about 20–25% of the eastern Bering Sea biomass (Hunt *et al*., 2010). Biomass and production of the western Bering Sea are dominated by pelagic nekton rather than demersal nekton (Shuntov and Radchenko, 1999).

The highly productive Bering Sea ecosystem also supports large populations of seabirds and marine mammals that enter the Bering Sea mainly during their summer feeding migrations but some islands, such as the Pribilof Islands and Commander Islands (see Fig. 4.5.1), are home to some breeding populations that spend the majority of their lives in the Bering Sea.

4.5.2 Jellyfish species composition

One of the earliest studies of eastern Bering Sea jellyfish was conducted as part of the Processes and Resources of the Bering Sea Shelf (PROBES) program by Hamner (1983). He noted that the Bering Sea, with its stable water masses, shallow shelf waters and high abundance of zooplankton in summer is an ideal region for supporting the production of dense populations of Scyphomedusae and Hydromedusae. Hamner (1983) used net tows, surface and SCUBA observations to determine the species composition, abundance, distribution and diets of medusae in July–August, 1982 with respect to water mass (oceanic, outer shelf, middle shelf and coastal domains). Twenty-two species of medusae were found, including 2 of which were Scyphomedusae, 7 were Anthomedusae and 7 were Leptomedusae. Certain medusae were associated with particular water masses. Numerous species of Hydromedusae occurred at high densities in the outer shelf domain, whereas a different assemblage of hydromedusae occupied the middle and coastal shelf waters. Four large species of medusae were conspicuous in the region: Scyphomedusae *Chrysaora melanaster*, the largest and most abundant, dominated the biomass in the outer and middle shelves, whereas *Cyanea* sp. and Hydromedusae *Aequorea* sp. and *Staurophora mertensii* occupied the oceanic and outer shelf waters. Hydromedusae and scyphomedusae formed dense aggregations of up to 1000 m^{-3} in surface convergences, apparently produced by Langmuir circulation (Hamner and Schneider, 1986). However, these medusae also occurred at depth in diving surveys, particularly in the mid-water near the pycnocline (~35 m), but at lower densities, *e.g.*, 0.02 *C. melanaster* m^{-3} (Hamner, 1983).

Coyle and Cooney (1993) conducted hydroacoustic and net studies within an approximate 130-km radius of the Pribilof Islands during the summers of 1987 and 1988. They found a general pattern of high acoustically determined biomass (ADB) in the upper 30 m and in epibenthic layers 15–20 m above the bottom but found little biomass in between the two layers. The upper layer ADB consisted of primarily large medusae, namely, *C. melanaster*, *S. mertensii* and *Aequorea* sp. while smaller medusae, such as Hydromedusae *Euphysa flammea*, *S. princeps* and *Catablema* sp., were numerically abundant. Overall, the average biomass (g m^{-3}) of cnidarians was 1.431 (±4.040 SD) in the midwater layer, 8.905 (±15.804 SD) in the surface-scattering layer at night, and 0.952 (±2.030 SD) in the epibenthic scattering layer. The cnidarian biomass in the upper water column was often associated with specific hydrographic features, such as salinity and temperature fronts near the islands, which may have concentrated the medusae as well as their prey.

Coyle *et al*. (2008) estimated cnidarian biomass with a 1 m^2, 500 µm-mesh MOCNESS near the Pribilof Islands and on the middle shelf of the eastern Bering Sea in August 1999 and 2004. Between these two periods, significant declines were observed in the biomass of large scyphomedusae such as *C. melanaster*, as was also apparent in shelf-wide trawl surveys (Brodeur *et al*., 2008b). By contrast, higher densities of small hydromedusae such as *E. flammea* were observed in 2004 relative to 1999. Shifts in the crustacean community were also observed over this period, as were changes in the diet of age-0 walleye pollock from large to small copepods in 2004 relative to 1999. Warmer conditions and increased water column stability in summer 2004 may have influenced the zooplankton community by decreasing primary production and selecting for species more tolerant of warmer, oligotrophic conditions.

Previously unpublished information on regional species composition from the Coyle *et al*. (2008) study is reported in Table 4.5.1. There are trends in the data by domain: Inner (≤50 m bottom depth), Middle (>50 and ≤150 m) and Outer (>150 m). Some taxa did not occur in the Inner domain (*e.g.*, *Aegina*, *Dimophyes* and *Ptychogena*) and others did not occur in the outer domain (many of the hydromedusae and some of the scyphomedusae). *Periphylla* is an oceanic animal so its absence from the Middle and Inner domains is expected. Similarly, although the ANOVA determines that *Rathkea* biomass differs among regions, the Bonferonni comparison indicates that this species does not exhibit any significant differences among the pairs. Thus, we can conclude that there were no significant differences in *Rathkea* biomass among domains.

Table 4.5.1 Mean biomass (g 1,000 m^{-3}) of major gelatinous zooplankton taxa from MOCNESS tows in the eastern Bering Sea, from July–August 1997–1999 and 2004, by domain (Inner (≤50 m bottom depth), Middle (>50 and ≤150 m) and Outer (>150 m).

Genus*	Inner	Middle	Outer	P-value	Bonferroni
Aegina	0	<0.01	0.04	<0.01	*O > I & M*
Aequorea	2.89	27.21	0.32	<0.01	*M > I*
Aglantha	2.47	1.61	8.02	<0.01	*O>M & I*
Aurelia **	92.82	159.93	0.03	0.61	
Bougainvillea	0.45	0.04	0	<0.01	*I > O = M*
Calycopsis	0	<0.01	0.25	<0.01	*O > I = M*
*Chrysaora***	1392.01	2203.49	0	<0.01	*M > I > O*
Corymorpha	0.27	4.31	0.01	<0.01	*M > I = O*
Coryne	1.90	0.16	0.32	<0.01	*I > M = O*
Cuspidella	0.29	5.99	0	0.65	
Cyanea **	2.56	4.28	0	0.18	
Dimophyes	0	0.01	0.81	<0.01	*O > M = I*
Eirene	4.65	2.15	0.15	0.01	*I = M > O*
Eperetmus	0	<0.01	0	0.69	
Gonionemus	<0.01	0.11	0	0.22	
Lar	0.04	0.01	0	0.24	
Melicertum	0.01	0.01	0	0.22	
Obelia	0.06	0.02	0	<0.01	*M > O = I*
Peachia ***	<0.01	<0.01	0	0.93	
Perigonimus	4.63	6.79	0	<0.01	*I = M > O*
Periphylla **	0	0	0.93	<0.01	*O > I & M*
Phacellophora **	0.24	1.72	0.70	0.32	
Phialidium	0.29	1.43	0	0.52	
Polyorchis	0.01	0.07	0	0.87	
Ptychogena	0	0.03	0.02	0.14	
Rathkea	0.01	<0.01	0.03	0.02	*I = M = O*
Stomotoca	0.10	<0.01	0	0.43	
Tiaropsis	0.51	<0.01	0	0.57	

The values were raised to the power of 0.15 for computing the ANOVAs, but the means reported here are arithmetic untransformed values. P-values indicate significant differences via ANOVA at level ≤0.05. The Bonferroni method compares mean biomass among domains, where *I* is Inner, *M* is Middle and *O* is Outer.

* Taxa are classified as Hydromedusae unless otherwise specified.

** Scyphomedusae

*** Anthomedusae

4.5.3 Spatial patterns in jellyfish biomass

Large-scale surveys of jellyfish in the Bering Sea

Determining trends in jellyfish biomass is difficult due to there being very few cases of large coverage annual surveys, past or present, being conducted for the sole purpose of targeting macro jellyfish (Purcell, 2009). In the Bering Sea, data collected from trawl surveys targeting fish have been used to determine macro jellyfish biomass (Brodeur *et al*., 2002, 2008a). In particular, three different surveys, described below, utilized different gear (surface and bottom trawls) and sampled locations with some to no overlap. Survey coverage included both the western Bering Sea and eastern Bering Sea (Fig. 4.5.1), which for the purposes of comparison were split into four regions: Northeast, Southeast, Northwest, and Southwest. The Southeast region encompasses the area between the Alaska Peninsula to 400 km north, extending east to the 20 m isobath and west to the 200 m isobath. The Northeast region's southern boundary parallels the Alaska Peninsula, starting from the 200 m isobath, running north of St. Paul Island (Pribilof Islands) ending in line with the town of Kipnuk. The north and west boundary coverage is from the 200-m isobaths running along the U.S. exclusive economic zone (EEZ) to 64.5°N, and extends to the 20-m isobaths and includes Norton Sound. The Northwest region includes the Gulf of Anadyr and adjacent shelf areas which extends southeast to the Russian EEZ border and southwest to the 200-m isobaths. The southwest region is primarily a deep water area that ranges from the Commander Islands along the EEZ border to the northwest region in the north.

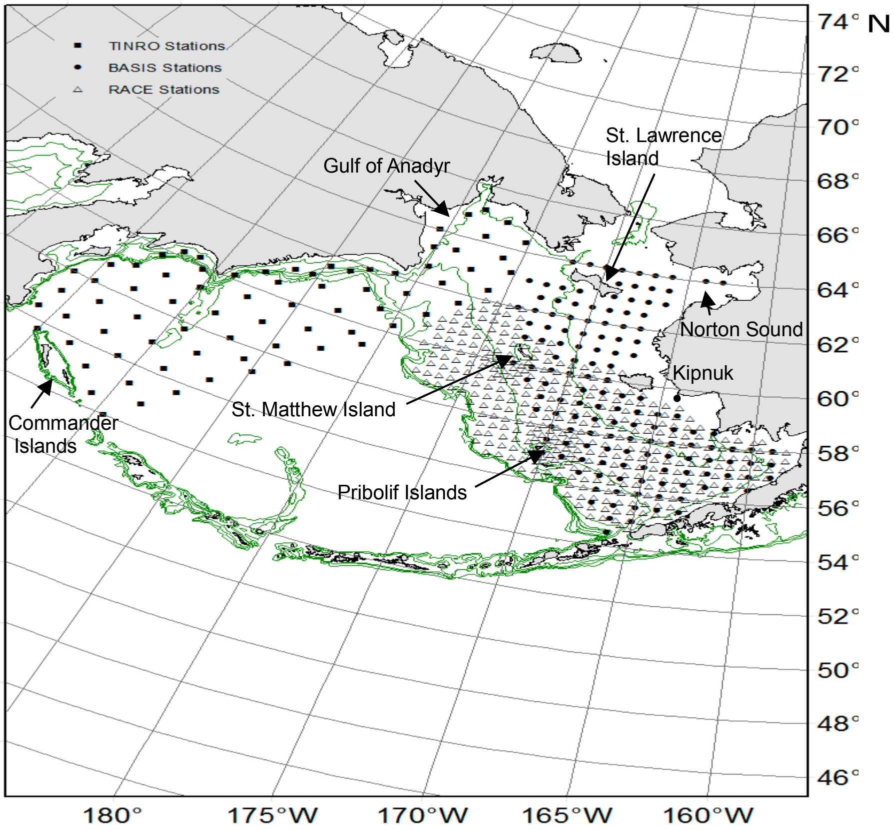


Fig. 4.5.1 Station map of annual Bering Sea surveys. The main portion of map displays Russian TINRO-Center, U.S. RACE, and U.S. BASIS research cruises. Closed circles = BASIS, Open triangles = RACE, Closed squares = TINRO-Center.

RACE Surveys

The Resource Assessment and Conservation Engineering (RACE) Division of the Alaska Fisheries Science Center (AFSC) has been conducting annual summer bottom trawl surveys to determine the condition of ground fish and invertebrates in the eastern Bering Sea since 1979. The sample area includes coverage from the Alaska Peninsula north to 60°50′N, extending out to the 200 m isobath. The sampling is on a grid system with fixed stations at the center of each 20 × 20 nautical mile square. The trawl is towed on the bottom for 30 minutes. Catches of all large jellyfish (bell diameters >50 cm) are weighed at sea and standardized to kg ha^{-1} (see Brodeur *et al*., 2008a for details). Species composition of the catch has only been determined for jellyfish since 2005.

BASIS Surveys

The Bering-Aleutian Salmon International Survey (BASIS) surface trawl surveys have been conducted annually by the AFSC since 2002, targeting forage fish and invertebrates from mid-August to early October. The sampling grid covers the shelf off western Alaska, from 159°W to 174°W longitude and 54.5°N to 64°N latitude. All stations are approximately 30 nautical miles (55.6 km) apart. All tows are standardized for gear (50 m wide by 18 m deep) and duration of tow (30 minute tows covering 2.8 to 4.6 km). Fish and jellyfish are collected using a mid-water rope trawl at or near the surface, with typical spreads of 66.4 m horizontally and 14.6 m vertically (see methods in Cieciel *et al*., 2009). All sampling is performed during daylight hours.

TINRO Surveys

Data from the western Bering Sea are derived from epipelagic trawl surveys that the TINRO-Center (Pacific Scientific Research and Fisheries Center, Vladivostok) conducted from 1991–2011. All 20 surveys were carried out in the Russian EEZ beyond the 12-mile territorial seas. Most of the surveys were conducted in summer (11 surveys, 925 tows) and fall (13 surveys, 984 tows). Only three surveys (81 tows) were performed in winter. Jellyfish were caught using large pelagic trawls with a vertical opening of 30–60 m and a horizontal opening of 28–52 m and equipped with a 1-cm mesh cod end liner (see methods in Volvenko (1998) and Zavolokin *et al*. (2008)). No corrections were made for extrusion of jellyfish through the larger mesh of the trawl nets; therefore the estimations of jellyfish biomass and abundance are substantially underestimated.

4.5.4 Regional interannual variability

Bering Sea surveys by Russian and U.S. fisheries agencies (*i.e*., NOAA's RACE and BASIS, and TINRO-Center) have reported on jellyfish species composition from the early 2000s to the present for both the western and eastern side of the Bering Sea (Figs. 4.5.2–4.5.4). The eastern Bering Sea can be readily described as being dominated by *C. melanaster*; surveys have reported high catches of the species, especially in recent years (Fig. 4.5.2). Summer and fall jellyfish species proportions in the eastern Bering Sea are very similar and since 2008, increases have been observed in the numbers of large jellyfish species present in reported survey catches, with *Aequorea* sp. and *Cyanea* sp. being two species that were once present in higher abundances than in recent years.

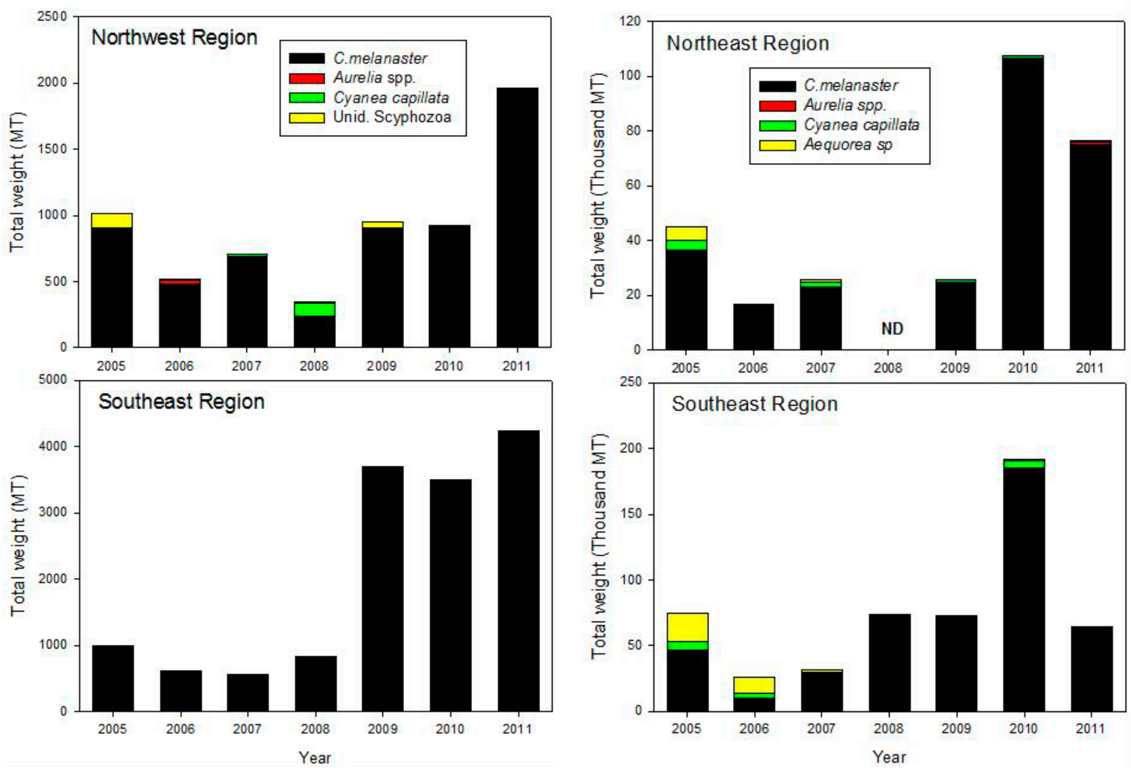


Fig. 4.5.2 Interannual comparison of the dominant species collected in summer during U.S. RACE bottom trawl surveys (left panels) and in fall during the U.S. BASIS research cruises (right panels). Jellyfish biomass units, in metric tons (MT), are for the RACE surveys and 1000 MT for the BASIS surveys, ND = no cruise. Note difference in scales. (from Decker *et al*., 2014).

In the western Bering Sea, trends for macro jellyfish species indicate an overall decline in biomass over the period 2000–2011 (Fig. 4.5.3). These patterns persist when the TINRO-Center survey data are plotted by season (Fig. 4.5.4). The eastern Bering Sea exhibits the opposite pattern for the same period, showing dramatic increases in the summer for the Southeast and in the fall for the Northeast regions (Fig. 4.5.2); biomass remains steady in the Northeast in summer and in the Southeast regions in fall. The western side of the Bering Sea differs from the eastern side in that its jellyfish species composition is more varied. In the Southwest, highest abundances are seen in *Aequorea* sp., *C. melanaster*, and most recently, *Phacellophora camtschatica* (Fig. 4.5.4). Northwest waters were dominated by *C. melanaster*, though in recent years species compositions are unknown due to lack of surveys.

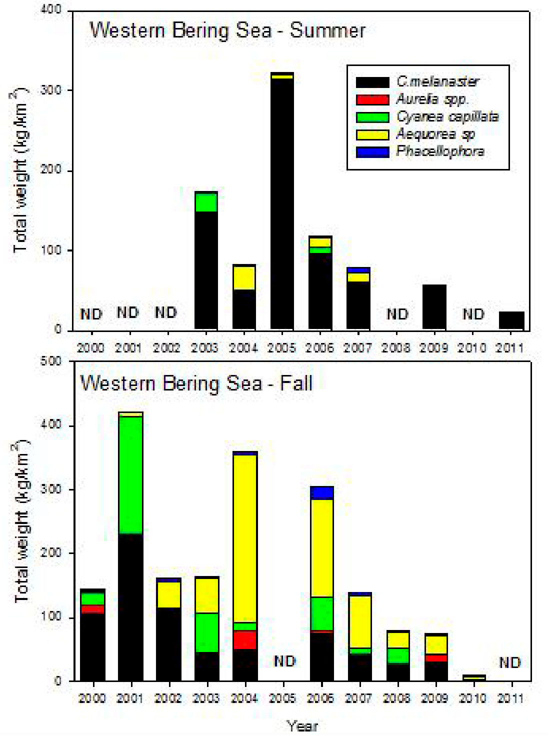


Fig. 4.5.3 Jellyfish biomass (kg km^{-2}) for the dominant species by season (summer, upper; fall, lower) during TINRO-Center research cruises. ND = no cruises done that year (from Decker *et al*., 2014).

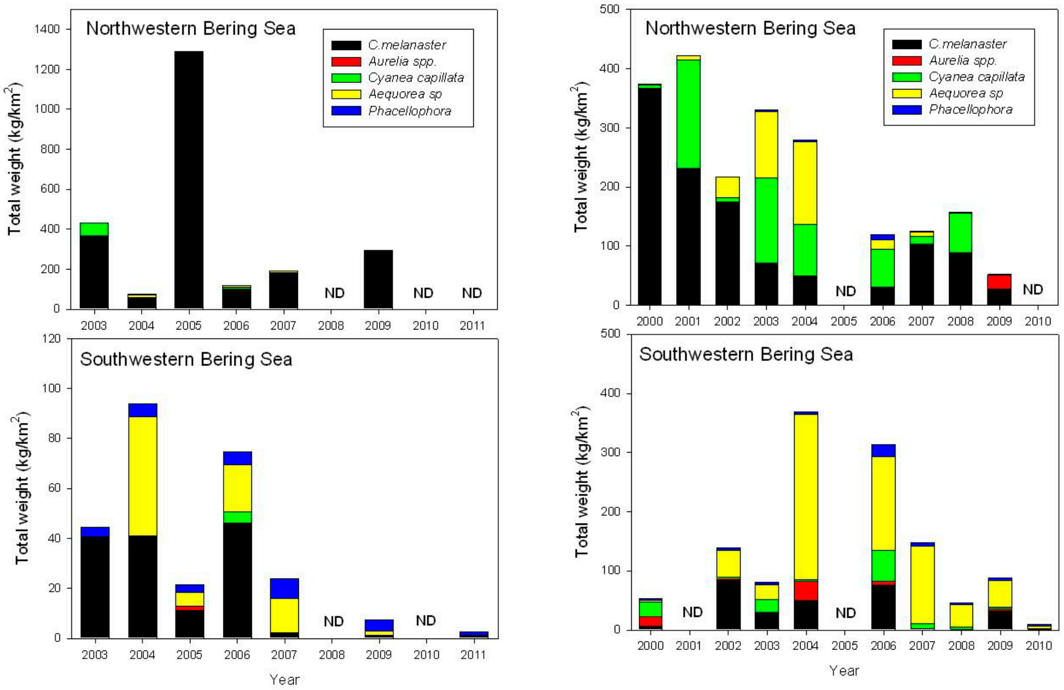


Fig. 4.5.4 Interannual comparison of summer (left panels) and fall (right panels) jellyfish biomass for the dominant species by geographic area from TINRO-Center research cruises. ND = no cruises done that year. Note differences in scales (from Decker *et al*., 2014).

Table 4.5.2 The mean biomass (kg km^{-2} ± SE) of jellyfish in the epipelagic layer of the western Bering Sea during 1991–2011 by season (from Decker *et al*., 2014).

Class – species	Summer	Fall	Winter
Scyphozoa	111.6 ± 18.2	87.1 ± 9.3	7.5 ± 1.5
Aurelia sp.	0.2 ± 0.1	5.0 ± 1.6	–
Chrysaora melanaster	105.4 ± 18.1	54.7 ± 8.4	5.1 ± 1.4
Cyanea sp.	3.0 ± 0.7	23.0 ± 3.3	0.1 ± 0.1
Phacellophora camtschatica	2.8 ± 0.2	4.2 ± 0.3	1.6 ± 0.7
Hydrozoa	8.6 ± 1.2	53.0 ± 4.6	0.6 ± 0.2
Aequorea sp.	8.5 ± 1.2	52.7 ± 4.6	0.5 ± 0.2
Number of stations	868	1074	81

4.5.5 Seasonal patterns

It is generally assumed that most of the large scyphomedusae have annual life cycles and the medusa stage dies after reproduction sometime during the fall or early winter. Although there are few winter surveys available from the Bering Sea because of the extended sea ice, there have been wintertime observations of jellyfish along the ice edge and some large and apparently overwintering jellyfish have been observed there in May (G.L. Hunt, University of Washington, pers. comm.), but this may be a rare occurrence.

The western Bering Sea is heavily dominated by *C. melanaster* in summer (Figs. 4.5.3 and 4.5.4, Table 4.5.2). Fall brings some change, with *C. melanaster* biomass starting to decline whereas other large jellyfish, *e.g.*, *Aequorea* sp. and *Cyanea* sp. increase in biomass. The eastern Bering Sea surveys have recorded *C. melanaster* at high levels of abundance and in recent years few other large jellyfish species have been caught (Fig. 4.5.2).

4.5.6 Horizontal distribution

Significant changes in the distribution large medusae have been observed during the summer RACE surveys in the eastern Bering Sea since the start of this time series in the early 1980s, with a dramatic distributional shift occurring after 1990, as indicated by a constrained zero-inflated generalized additive model (Liu *et al*., 2011). In the early period of low jellyfish biomass (1982–1989), the largest biomass was mainly in the southern part of the survey area, over the middle shelf (Fig. 4.5.5). During the first escalating phase (1990–2000), jellyfish biomass increased in the northern part of the survey area, also on the middle shelf. At the peak (2000, Fig. 4.5.6), biomass was high in both the north and south portions of the middle shelf and extended into the southern inner (<50 m depth) shelf region. During an unusual period of warming in the Bering Sea, and declining jellyfish biomass (2001–2005), concentrations of jellyfish were located near the Alaska Peninsula and northwest of the Pribilof Islands (Fig. 4.5.5).

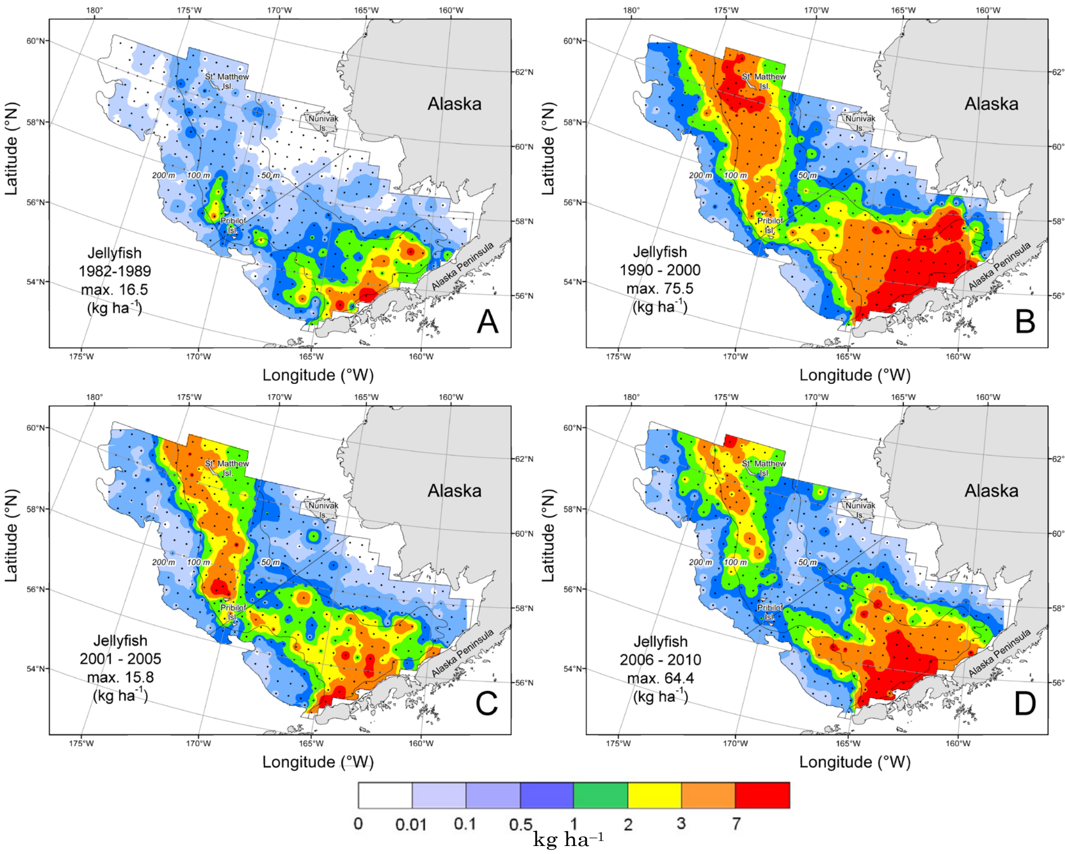


Fig. 4.5.5 Spatial distributions during the RACE eastern Bering Sea surveys of average jellyfish biomass (kg ha^{-1}) for the periods (A) 1982–1989, (B) 1990–2000, (C) 2001–2005 (an anomalously warm period), and (D) 2006–2010 (a very cold period) (from Decker *et al*., 2014).

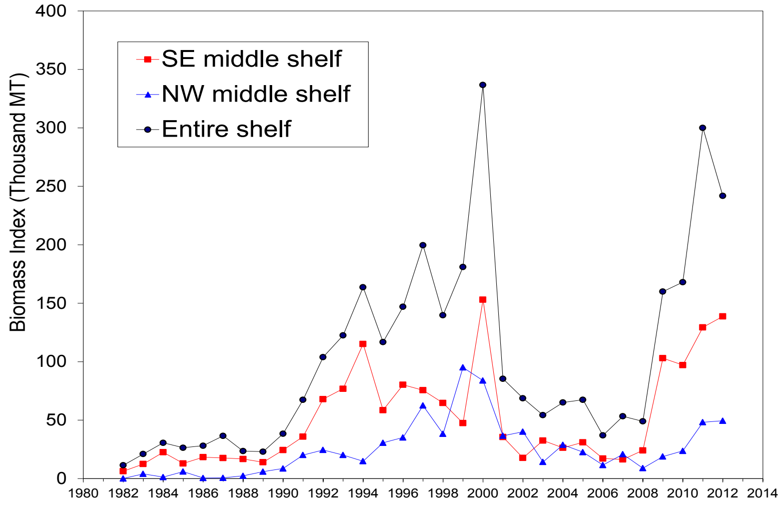


Fig. 4.5.6 Trend in jellyfish biomass from standardized bottom trawl surveys in the Bering Sea since 1982. Shown are the total biomass (black line) and subsets for the Southeast (SE, red) and Northwest, (NW, blue) middle shelf domains (modified from Decker *et al*., 2014).

Large jellyfish were observed during fall BASIS surveys in the eastern Bering Sea, starting with 2004 catch data when reporting began to include jellyfish species. Combined jellyfish species distribution for averaged warm years 2004 and 2005 showed evenly distributed jellyfish catches across the middle shelf in both the Northeast and Southeast regions (Fig. 4.5.7). During warm years, relatively high catches were observed in the north (above 60°N) and lower catches in the inner and outer shelves. The cold year average for 2006–2010 distribution varied but was consistent with the warm years showed evenly distributed catches in the middle domain and lower catches in the south portion of the inner and outer shelves (Fig. 4.5.7). Based on surveys in the fall, the highest concentrations of combined jellyfish catch occurred in the areas around Saint Lawrence Island for both warm and cold years.

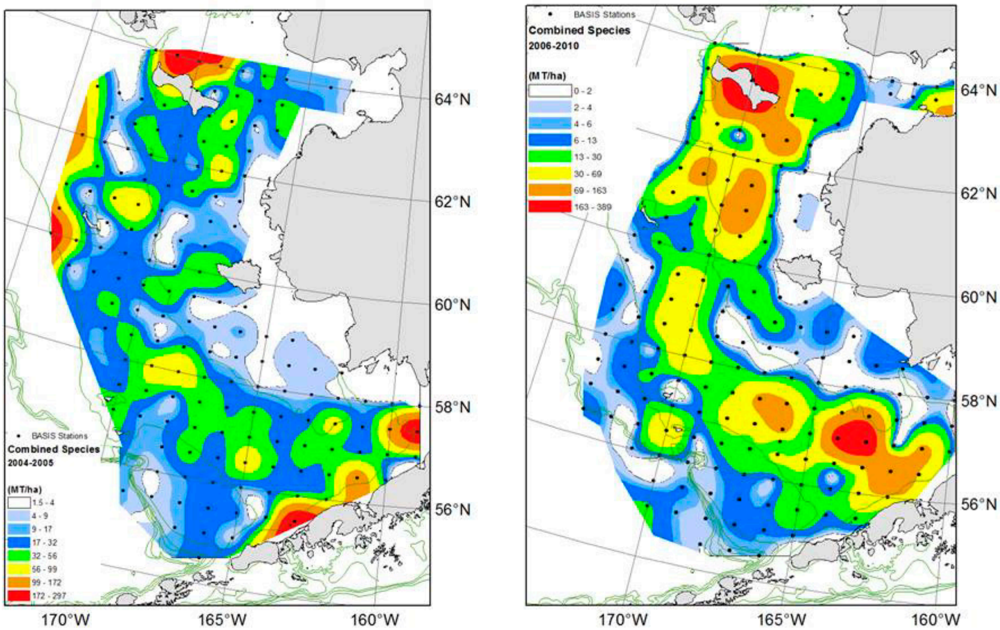


Fig. 4.5.7 Spatial distributions of average biomass (metric tons, MT ha^{-1}) in warm (2004–2005, left) and cold (2006–2010, right) years from the BASIS eastern Bering Sea surveys (from Decker *et al.*, 2014).

In the western Bering Sea, the highest concentrations of jellyfish occurred on the shelf near the Gulf of Anadyr and in adjacent waters (Fig. 4.5.8). Jellyfish biomass reached a maximum in summer due to high numbers of the large *C. melanaster* at that time of year. In deep-water regions, the relative biomass of jellyfish was generally lower than that on the shelf, declining with increasing distance offshore (Fig. 4.5.8).

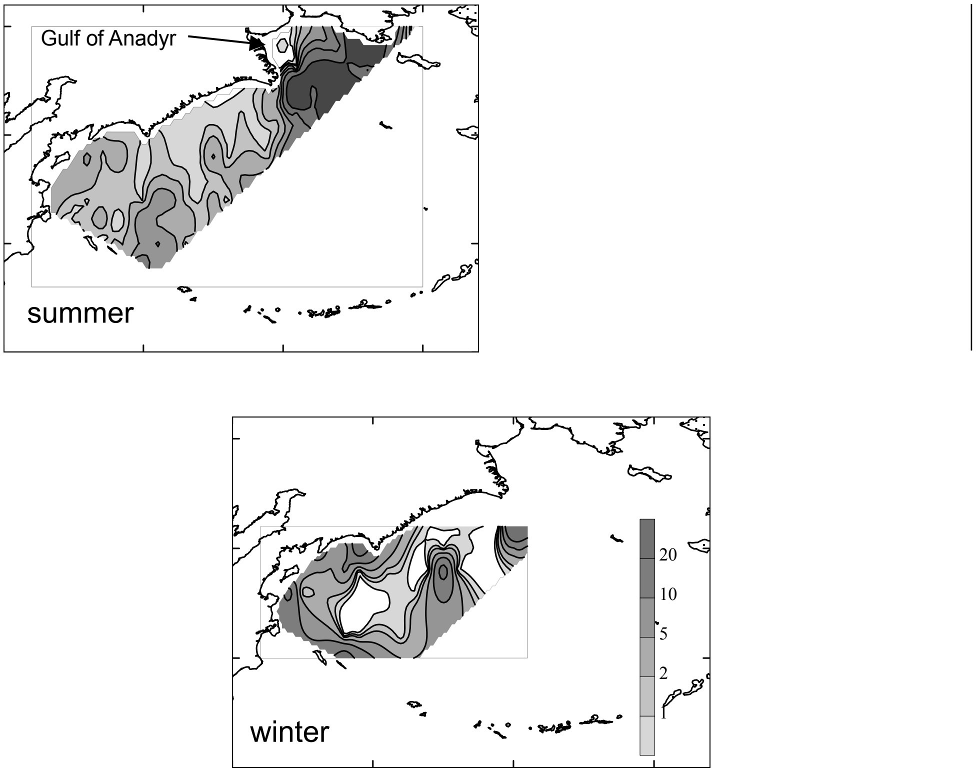


Fig. 4.5.8 Distribution of total jellyfish biomass (kg km^{-2}), predominantly *Chrysaora*, *Cyanea*, and *Aequorea*, combined for all years (1991–2011), by season from TINRO-Center research cruises. Note the difference in scales and that the winter surveys do not extend as far north due to the presence of seasonal sea ice (from Decker *et al*., 2014).

The dominant species *Chrysaora*, *Cyanea*, and *Aequorea* had different distribution patterns. *Chrysaora melanaster* was widespread throughout the western Bering Sea, but was the most numerous on the outer shelf off the Gulf of Anadyr (Fig. 4.5.9). *Chrysaora melanaster* concentrations decreased from summer to fall on the shelf region but increased in the deep-water areas. *Cyanea* sp. inhabited mostly shallow regions of the Gulf of Anadyr in summer but was found along the entire coast in the fall, where it had the highest biomass. Concentrations of *Cyanea* sp. decreased sharply from the shelf to deep-water basins. *Aequorea* sp. was concentrated mainly in the deep-water regions in the summer but by fall its distributional area was more widespread and it became very abundant in the shallower waters of the Gulf of Anadyr.

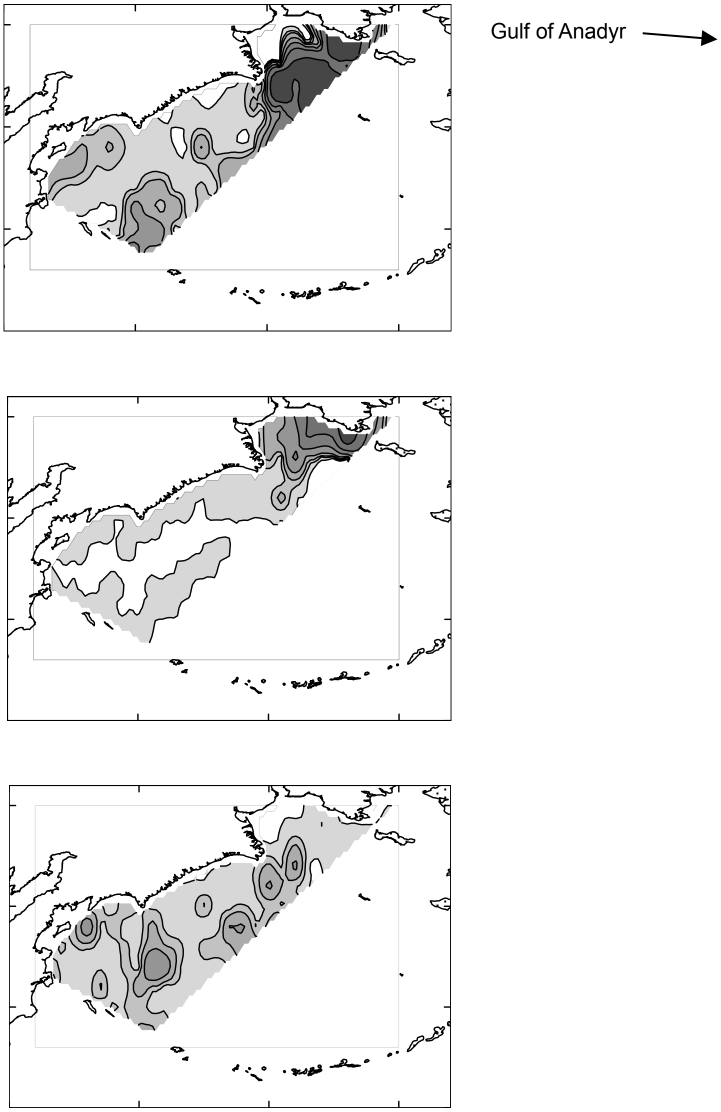


Fig. 4.5.9 Distribution of biomass (kg km^{-2}) of *Chrysaora* (top), *Cyanea* (middle) and *Aequorea* (bottom) in the western Bering Sea for all years combined (1991–2011), by summer (left panels) and fall (right panels) from TINRO-Center research cruises (from Decker *et al*., 2014).

Basin-wide distribution patterns

During August and September of 1987, large-scale pelagic fish and invertebrate surveys were conducted in the western and eastern Bering Sea, except for international waters in the center (*i.e*., “Donut Hole”), by the Russian research vessels R/V *Darwin* and R/V *Gnevny* (Fig. 4.5.10). Although the gear was slightly different during the two surveys, catch data were standardized to the same sampling area and to weight per hour towed (see Brodeur *et al*., 1999 for detailed sampling methodology). Cnidarians were the most frequently-occurring taxa in both the eastern (139 out of 149 tows) and western (150 out of 183 tows) Bering Sea. They were second most important (after age 2+ walleye pollock) in mean biomass in the survey in the eastern part and fourth in the western part of the survey (Brodeur *et al*., 1999). Basin-wide, overall jellyfish biomass was substantially higher in the eastern Bering Sea, concentrated mainly on the shelf north of the Alaskan Peninsula (Fig. 4.5.10) although most stations recorded jellyfish. This distributional pattern is similar to what was seen during the RACE surveys in the late 1980s (Fig. 4.5.5).

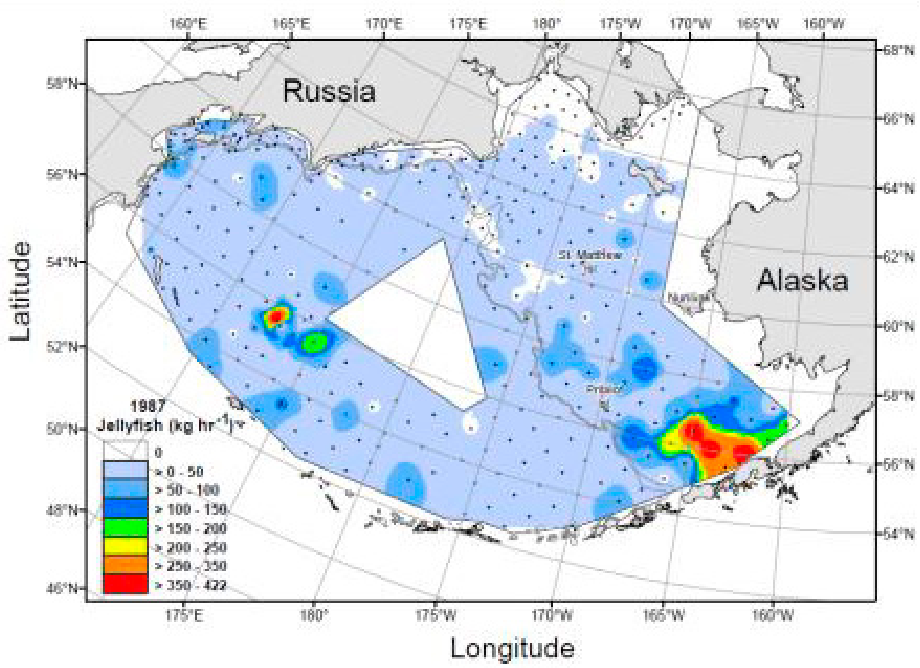


Fig. 4.5.10 Inverse Distance Weighted (IDW) plot combining the 1987 R/V *Darwin* and R/V *Gnevny* jellyfish catches (kg hr^{-1}). The trapezoid polygon in the middle of the map designates the "Donut Hole" where there was no sampling (from Decker *et al*., 2014).

4.5.7 Vertical distribution

During the TINRO-Center surveys, a single station was occupied in the southwestern Aleutian basin (58° N, 172° E) for 14 days on August 23–September 5, 2004 and 75 tows were conducted at depths 0, 40, 80, 120, 160, 200, 350, 500, and 750 m to examine the diel vertical distribution of cnidarians. There were 6 to 7 tows at each depth (from 0 to 750 m) within a 4-hour time span followed by an additional 13 tows in the surface layer (0 m). Jellyfish were found in all the layers trawled, from 0 to 750 m (Fig. 4.5.11). Highest concentrations overall occurred in the upper epipelagic zone (0–50 m). Biomass and abundance of jellyfish decreased tenfold from the surface to the lower layers (50–200 m). By contrast, jellyfish abundance increased steadily from 400 m down to the deepest layer (750 m) trawled.

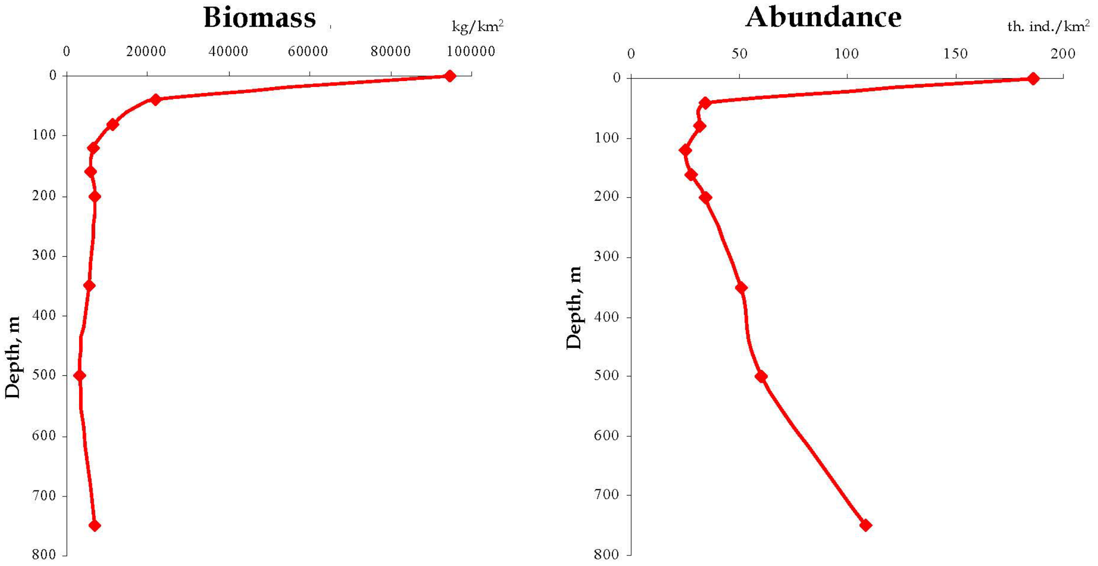


Fig. 4.5.11 Vertical distribution of total jellyfish biomass (lef) and density right) at a diel station in the western Bering Sea in 2004 for all jellyfish species combined (adapted from Decker *et al*., 2014).

Only three (*C. melanaster, Aequorea* sp. and *Calycopsis nematophora*) of eight jellyfish species occurred at all depths throughout the water column from 0 to 750 m (Table 4.5.3). *Chrysaora melanaster* and *Aequorea* sp. were abundant in the surface layer and their biomass and abundances generally decreased from the surface to deep layers (except at 350 and 500 m depth for *C. melanaster* and 750 m depth for *Aequorea* sp.), whereas *C. nematophora* had the highest concentrations in upper mesopelagic (200–1000 m) zone. *Phacellophora camtschatica* and *Periphylla periphylla* also had a wide vertical distribution but were missing from some depth intervals. *Phacellophora camtschatica* was more numerous in the epipelagic zone, whereas *P. periphylla* concentrated mainly in mesopelagic zone. Only *Aurelia* sp. inhabited exclusively epipelagic waters, and was generally confined to the surface layer. *Atolla wyvillei* was found the deep mesopelagic layers, occurring at 350, 500 and 750 m. Biomass and abundance of *A. wyvillei* increased sharply from the upper to lower layers and it is possible that high numbers of this species were concentrated below the maximum depth of sampling, 750 m. *Ptychogena lactea* occurred in the lower epipelagic and in the mesopelagic zones, from 120 to 750 m, and was most abundant in the upper layers of the mesopelagic zone. Overall, *Aequorea* sp., *C. melanaster* and *Aurelia* sp. were the dominant species in terms of biomass and abundance in the epipelagic zone. *Aequorea* sp., *C. melanaster* and *A. wyvillei* were also present at high biomasses in mesopelagic layer. *C. nematophora, P. periphylla* and *A. wyvillei* were abundant at depth.

Table 4.5.3 Vertical distribution (depth in m) of mean ± SE jellyfish biomass (kg km^{-3}) and abundance (1000 individuals km^{-3}) of the dominant species at a diel station in the western Bering Sea in 2004 (from Decker *et al*., 2014).

Depth	***Atolla wyvillei***	***Aurelia* sp.**	***Chrysaora melanaster***	***Periphylla periphylla***	***Phacellophora camtschatica***	***Aequorea* sp.**	***Calycopsis nematophora***	***Ptychogena lactea***	**Tows**
	Biomass								
0	–	2860 ± 1794	2847 ± 433	–	169 ± 53	3557 ± 824	3.5 ± 1.7	–	20
40	–	–	1017 ± 226	1.2 ± 1.2	208 ± 78	954 ± 374	0.9 ± 0.8	–	7
80	–	70 ± 61	193 ± 97	0.1 ± 0	158 ± 59	694 ± 210	3.4 ± 2.5	–	7
120	–	–	56 ± 24	2.5 ± 2	51 ± 47	539 ± 182	4.5 ± 2.8	0.7 ± 0.4	7
160	–	–	84 ± 48	–	7.3 ± 4.2	478 ± 142	7.2 ± 4.5	0.2 ± 0.1	7
200	–	–	234 ± 74	2.7 ± 2.2	–	448 ±113	8.4 ± 3.1	0.6 ± 0.4	7
350	1 ± 1	–	146 ± 79	6.5 ± 3.4	2.3 ± 1.7	387 ± 117	11.6 ± 3.8	0.5 ± 0.1	6
500	12 ± 5	–	44 ± 31	31.2 ± 10.7	14.2 ± 11.7	207 ± 52	3.5 ± 0.8	0.4 ± 0.2	7
750	129 ± 26	–	31 ± 16	48.6 ± 14.9	13.7 ± 9.7	460 ± 124	3.9 ± 0.8	0.3 ± 0.2	7
	Abundance								
0	–	5533 ± 3631	3086 ± 522	–	283 ± 73	8651 ± 1806	1060 ± 515	–	20
40	–	–	799 ± 130	55 ± 55	180 ± 86	2123 ± 855	261 ± 240	–	7
80	–	163 ± 142	184 ± 88	18 ± 18	287 ± 147	1530 ± 478	1009 ± 728	–	7
120	–	–	95 ± 39	74 ± 55	78 ± 50	946 ± 255	1161 ± 722	148 ± 105	7
160	–	–	72 ± 37	–	73 ± 37	896 ± 242	1685 ± 1073	37 ± 24	7
200	–	–	191 ± 54	168 ± 117	–	780 ± 122	2214 ± 812	109 ± 72	7
350	73 ± 36	–	165 ± 61	916 ± 481	75 ± 38	921 ± 245	2847 ± 888	111 ± 29	6
500	789 ± 375	–	34 ± 22	3128 ± 1165	48 ± 33	577 ± 132	1340 ± 241	131 ± 75	7
750	4056 ± 1149	–	47 ± 23	2639 ± 837	163 ± 123	2484 ± 1020	1325 ± 331	130 ± 112	7

Dashes indicate zero catch.

4.5.8 Diel vertical migration

The TINRO-Center surveys also found that *C. melanaster, P. camtschatica* and *Aequorea* sp. were concentrated mainly in the upper 120 m during day and night (Fig. 4.5.12a,b,c) and did not appear to migrate extensively. Most of the *C. melanaster* and *Aequorea* sp. inhabited the surface layer, whereas *P. camtschatica* had high concentrations deeper in the water column in the two depth strata below the surface. In contrast, the diel vertical distributions of *P. periphylla*, *C. nematophora* and *P. lactea* clearly show that they migrated up from mesopelagic depths to the surface during the nighttime and migrated down during the daytime (Fig. 4.5.12d,e,f). The broadest range of distribution was shown by *C. nematophora* which showed a high biomass in deeper waters up to 750 m in the daytime and primarily in surface waters at night. *Periphylla periphylla* ascended to only the 40 m layer at night, and was not caught in surface waters. *Periphylla periphylla* showed the highest biomass at 500 and 750 m during both at day and night (Fig. 4.5.12d). *Calycopsis nematophora* was most abundant at 160–200 m in the nighttime and at 350 m in the daytime (Fig. 4.5.12e). *Ptychogena lactea* concentrated mainly at 120–200 m at night and at 500–750 m during daytime (Fig. 4.5.12f).

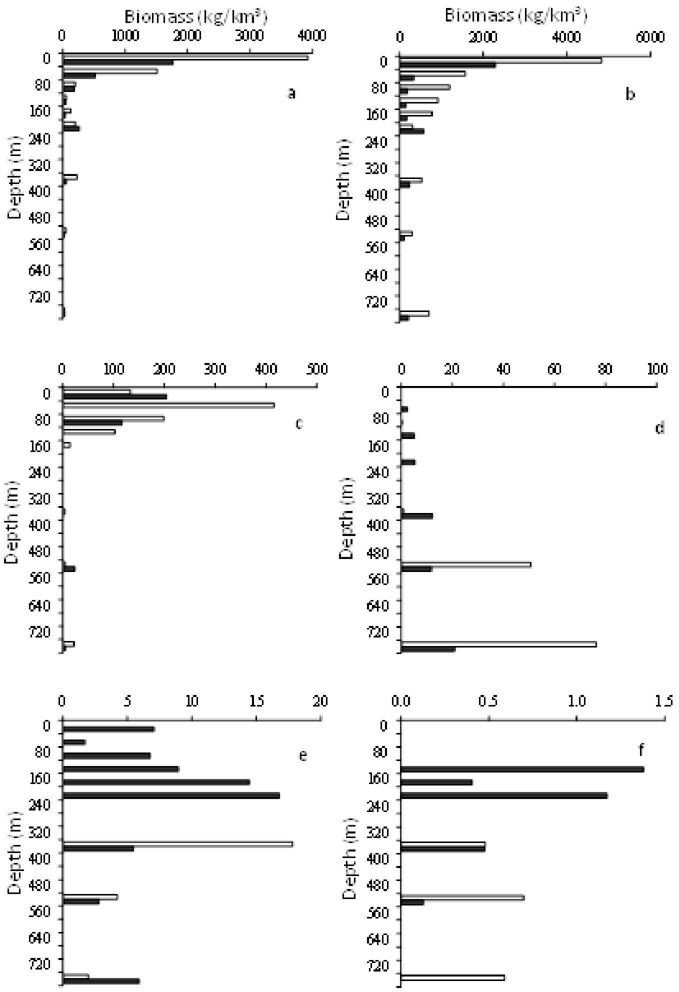


Fig. 4.5.12 Vertical profiles of jellyfish (kg km^{-3}) during day (open bars) and night (filled bars) by depth in the 0–750 m layer at a diel station in the western Bering Sea in 2004 for the dominant species: (a) *Chrysaora melanaster*, (b) *Aequorea* sp., (c) *Phacellophora camtschatica*, (d) *Periphylla periphylla*, (e) *Calycopsis nematophora*, (f) *Ptychogena lactea* (from Decker *et al*., 2014).

4.5.9 Jellyfish size in relation to depth

Evidence of changes in body size with depth occurred only for *P. camtschatica* in the western Bering Sea (Table 4.5.4). The mean, minimum and maximum bell diameter clearly decreased from surface to deep waters. Size ranges of *P. camtschatica* were 8–47 cm for medusae caught in the upper 200 m layer and 6–22 cm for medusae caught deeper. The average body size of *P. periphylla* was generally larger in the epipelagic (3–8 cm) than in mesopelagic zone (3–4 cm), suggesting that large medusae migrate more extensively at night. Bell diameters of *C. melanaster, Aurelia* sp. and *Aequorea* sp. were similar at most of depth layers and did not show any trends (Tables 4.5.4 and 4.5.5). Size ranges of these jellyfish were 10–44, 9–32 and 6–29 cm, respectively. The smallest individuals of *Aequorea* sp. (6–7 cm) occurred only at the deep layers (500–750 m). The high abundance of *Aequorea* sp. and *P. camtschatica* in the deep-water regions and the occurrence of small medusae mainly in mesopelagic layers suggest that the polyps of these species inhabit generally greater depths. No apparent differences in body size of *C. nematophora* and *P. lactea* were evident (Table 4.5.5), but these species are relatively small even as adult individuals and may not be adequately sampled by the net mesh size used.

Table 4.5.4 Vertical profiles of mean Scyphozoa bell diameter (cm) in the western Bering Sea in 2004 (from Decker *et al*., 2014).

Species	Depth (m)	Bell diameter (cm)	95% C.I.	Min.	Max.	N
Atolla wyvillei	350	4.5	1.1	4	6	4
	500	5.2	0.4	4	9	23
	750	6.5	0.4	2	13	48
Aurelia sp.	0	20.0	0.3	9	32	61
	40	–	–	–	–	–
	80	20.6	4.1	13	28	9
Chrysaora melanaster	0	25.2	0.5	14	44	278
	40	28.5	1.6	17	38	32
	80	27.5	3.4	23	35	9
	120	26.5	2.5	25	30	4
	160	27.3	15.2	15	38	4
	200	28.8	3.6	22	38	11
	350	23.1	7.4	10	32	7
	500	31.0	19.1	30	33	2
	750	23.2	10.0	19	26	3
Periphylla periphylla	0	–	–	–	–	–
	40	7.5	4.3	7	10	2
	80	2.5	–	–	–	1
	120	5.9	3.0	4	9	4
	160	–	–	–	–	–
	200	3.6	1.2	2	6	9
	350	2.6	0.3	2	6	30
	500	3.7	0.2	2	12	115
	750	4.4	0.3	2	9	57

Table 4.5.4 Continued.

Species	Depth (m)	Bell diameter (cm)	95% C.I.	Min.	Max.	N
Phacellophora camtschatica	0	20.2	2.6	8	47	40
	40	27.0	4.8	18	42	7
	80	21.4	3.8	9	37	9
	120	21.5	13.9	11	29	3
	160	11.5	38.1	9	15	2
	200	–	–	–	–	–
	350	7.0	4.8	6	12	4
	500	13.7	20.6	6	22	3
	750	10.7	2.6	7	16	6

Min = minimum diameter, Max = maximum diameter, N = number of individuals. Dashes indicate zero catch.

Table 4.5.5 Vertical profiles of mean Hydromedusae bell diameters (cm) in the western Bering Sea in 2004 (from Decker *et al*., 2014).

Species	Depth (m)	Bell diameter (cm)	95% C.I.	Min.	Max.	N
Aequorea sp.	0	18.9	0.1	12	29	143
	40	19.1	0.5	10	28	43
	80	19.1	0.7	14	27	41
	120	19.6	0.7	15	26	30
	160	20.0	0.8	15	28	35
	200	19.5	0.6	15	24	19
	350	19.3	1.0	14	27	29
	500	19.8	1.5	6	25	18
	750	13.6	0.9	7	25	74
Calycopsis nematophora	0	1.9	0.1	1	3	54
	40	2.1	0.2	2	3	4
	80	1.9	0.1	1	3	20
	120	2.0	0.1	1	3	28
	160	2.0	0.1	1	3	28
	200	1.9	0.1	1	3	41
	350	2.1	0.1	1	4	64
	500	1.9	0.1	1	3	66
	750	1.8	0.1	1	3	52
Ptychogena lactea	120	3.8	0.5	3	6	5
	160	3.9	7.6	3	5	2
	200	3.1	1.2	3	5	5
	350	3.7	0.9	3	5	6
	500	4.1	0.4	4	5	5
	750	4.4	0.1	4	5	2

Min = minimum diameter, Max = maximum diameter, N = number of individuals.

4.6 Okhotsk Sea

Elena Dulepova and Alexander Zavolokin

Pacific Scientific and Research Fisheries Center (TINRO-Center), Vladivostok, Russia

The Okhotsk Sea is located in the northwestern Pacific and is separated from the ocean by a chain of the Kuril Islands and Kamchatka Peninsula. To the south and west it is bounded by the coast of Hokkaido Island, eastern coast of Sakhalin Island and the coast of the Asian continent. The Okhotsk Sea is the coldest regional sea of East Asia. The average annual sea surface temperature varies from 2 to 3°C in the north and from 5 to 7°C in the south (Terziev, 1998). In winter, almost the whole sea, with the exception of the southeastern part, is covered with ice. For about four months, ice occupies more than 50% of the Okhotsk Sea. The average maximum of ice cover is more than 80% but during the most severe winters it reaches 98% (Shuntov, 2001). The Okhotsk Sea is the major cooling and freshening source for the intermediate waters of the North Pacific subarctic (Yasuda, 2004). In summer, the Okhotsk sea surface warms up to 18–19°C. However, the upper warm layer is relatively thin: 30–75 m. Under this layer down to about 150 m, the water remains very cold. Temperature of this cold intermediate layer can reach 1.7°C (Chernyavsky, 1992). Resulting from the contact of cold intermediate layer and sea bottom, the broad shelf areas in the north, west and northeast are occupied by cold water of below freezing temperature throughout the year. This affects the distribution and abundance of marine species and has a great importance for cnidarian polyps inhabiting the mid-shelf region. The main feature of the Okhotsk Sea circulation is a general cyclonic motion of waters (counter-clockwise) along the margins of the whole basin. Due to the warming effect of ocean water inflow, the southeastern Okhotsk Sea is relatively warm. The shelf region off Western Kamchatka is the most productive area of the Okhotsk Sea in terms of pelagic and benthic living resources, including jellyfish.

Jellyfish studies in the Okhotsk Sea began in the mid-20th century. They generally were concerned with taxonomy and distribution of jellyfish. Results of these studies were summarized by Naumov (1960, 1961). In the Okhotsk Sea, 10 species of free-swimming Scyphomedusae and 186 species of Hydromedusae were found. Estimates of large jellyfish abundance in the Okhotsk Sea based on trawl survey data were first provided by Shuntov *et al*. (1994). These authors showed that gelatinous zooplankton have a significant biomass and can play a pivotal role in pelagic communities. Since their publication, annual pelagic surveys by TINRO-Center have provided new information on the Okhotsk Sea jellyfish, much of which was published in several papers (Gorbatenko *et al*., 2005; Ilinsky and Zavolokin, 2007, 2011; Zavolokin, 2010a). Data on jellyfish composition, spatial distribution, migration, biomass and abundance were summarized by Zavolokin (2010b,c, 2011). In this Working Group report, data on jellyfish of the Okhotsk Sea were updated to 2012.

This section is based on data collected during 41 epipelagic surveys conducted by TINRO-Center in the Okhotsk Sea from 1991 to 2012. A total of about 4,700 trawls were made with the majority occurring in fall (43%), summer (24%) and spring (23%). Jellyfish exceeding 2 cm in diameter were retained in the large pelagic trawls (vertical opening 30–56 m and horizontal opening 28–50 m) used in the sampling which contained a small-mesh (1 cm) liner in the cod end. Smaller jellyfish were collected in a Juday net with a 0.1-m^2 mouth opening and a 0.168-mm mesh net.

For the period 1991–2012, 11 species of jellyfish were recorded. Of these, 7 species belonged to the class Scyphozoa (*Atolla wyvillei, Aurelia aurita* s.l., *A. limbata, Chrysaora melanaster, Cyanea capillata,* *Periphylla periphylla, Phacellophora camtschatica*) and 4 species belonged to the class Hydrozoa (*Aequorea* sp., *Calycopsis nematophora, Ptychogena lactea, Tima sachalinensis*). *Chrysaora melanaster* and *C. capillata* dominated the jellyfish biomass. They comprised 66–99% of the total biomass. In the fall, *A. limbata* became one of the dominant species in the northern Okhotsk Sea.

Overall, jellyfish were relatively widespread in the Okhotsk Sea (Fig. 4.6.1a). During the warm seasons (summer and fall), they were concentrated mostly in the shelf areas of Western Kamchatka and adjacent waters. They also showed high biomass in the central part of the Okhotsk Sea and inshore in the northern part. The distribution of jellyfish species showed different patterns. *Cyanea capillata* and *A. limbata* generally inhabited the shelf areas and had their highest concentrations at inshore stations (Fig. 4.6.1c, d). They were rare in the deeper water part of the sea. *Chrysaora melanaster* occurred both inshore and offshore but was the most numerous in the eastern and central Okhotsk Sea (Fig. 4.6.1b). In contrast, other jellyfish species were more abundant in deeper waters.

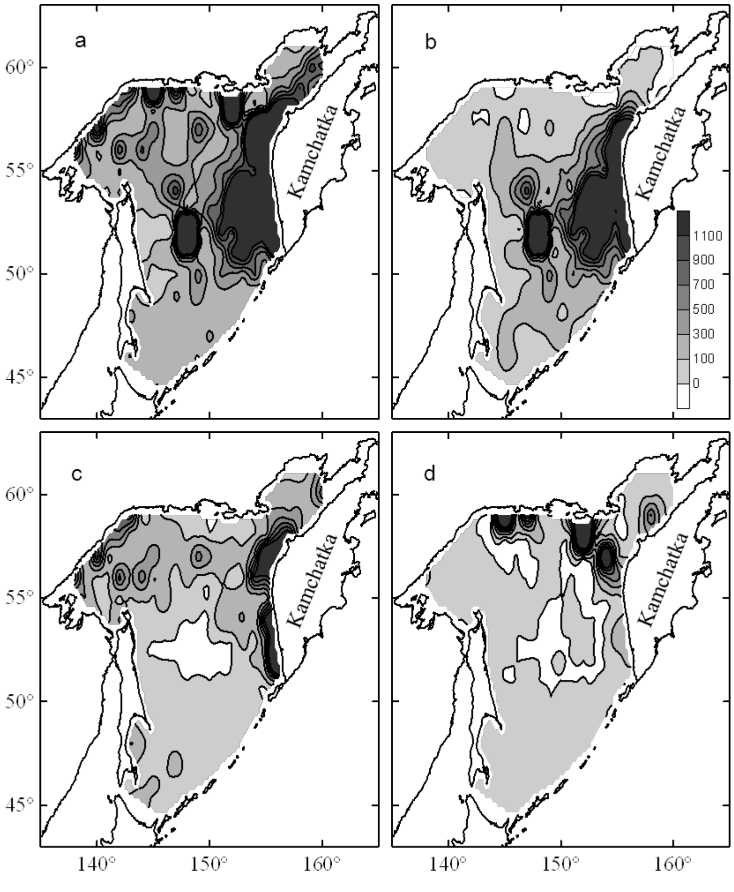


Fig. 4.6.1 Overall distribution of jellyfish (kg km^{-2}) in the Okhotsk Sea during the warm seasons (summer and fall) from 1990–2000s for (a) all species, (b) *Chrysaora melanaster*, (c) *Cyanea capillata* and (d) *Aurelia limbata*.

During the cold seasons (winter and spring), jellyfish distribution did not change markedly. However, their biomass decreased substantially in comparison with the warm seasons. The highest concentrations occurred in shelf regions of the eastern Okhotsk Sea (Fig. 4.6.1). Thus, the shelf region of the Western Kamchatka appears to be the main reproduction area of jellyfish in the Okhotsk Sea. Favorable conditions for polyp survival in this region continue throughout the year due to an inflow of warm water from the Pacific Ocean. In the northern shelf area, oceanographic conditions are much more severe. Prolonged ice cover (6–9 months) and cold near-bottom waters may negatively affect polyp survival and delay their strobilation.

Total jellyfish biomass increased from spring to summer in the epipelagic layer and then decreased to the lowest level in the winter in the southern Okhotsk Sea (Tables 4.6.1). However, the seasonal dynamics of different jellyfish species were not similar. In the Northern Okhotsk Sea, *C. melanaster* had the highest biomass in summer, *P. camtschatica* and *T. sachalinensis* peaked in the beginning of winter, and *C. capillata* and *P. lactea* were the most numerous in spring (Table 4.6.2). In the southern Okhotsk Sea, most jellyfish species reached their highest biomass in fall.

Table 4.6.1 Seasonal changes in jellyfish biomass (kg km^{-2}) in the epipelagic layer (0–200 m) of the southern Okhotsk Sea from 1991 to 2012. Data are mean biomass ± SE.

Taxon	**Summer (June–Aug.)**	**Fall (Sep.–Nov.)**	**Winter (Dec.–Feb.)**
Scyphozoa	174 ± 20	163 ± 15	30 ± 7
Aurelia aurita s.l.	–	1 ± 0.3	2 ± 2
Chrysaora melanaster	118 ± 16	61 ± 10	6 ± 2
Cyanea capillata	50 ± 8	91 ± 11	15 ± 5
Phacellophora camtschatica	3 ± 0.4	8 ± 2	7 ± 2
Hydrozoa	2 ± 1	12 ± 2	1 ± 0.3
Aequorea sp.	2 ± 1	11 ± 2	1 ± 0.3
Number of stations	585	411	158

Table 4.6.2 Seasonal changes in jellyfish biomass (kg km^{-2}) in the epipelagic layer (0–200 m) of the northern Okhotsk Sea from 1991 to 2012. Data are mean biomass ± SE.

Taxon	**Spring (April–May)**	**Summer (June–Aug.)**	**Fall (Sep.–Nov.)**	**Winter (Dec.–Feb.)**
Scyphozoa	558 ± 111	867 ± 91	742 ± 77	565 ± 82
Aurelia limbata	17 ± 4	2 ± 1	119 ± 42	6 ± 3
Chrysaora melanaster	176 ± 19	797 ± 90	291 ± 48	202 ± 38
Cyanea capillata	362 ± 109	64 ± 20	290 ± 34	212 ± 49
Phacellophora camtschatica	2 ± 1	4 ± 1	31 ± 7	55 ± 19
Hydrozoa	39 ± 7	7 ± 2	23 ± 3	63 ± 13
Ptychogena lactea	22 ± 7	2 ± 1	6 ± 1	10 ± 5
Tima sachalinensis	14 ± 3	5 ± 2	11 ± 2	42 ± 12
Number of stations	998	540	1310	352

In the mesopelagic zone, the abundance of jellyfish also changed seasonally (Zavolokin, 2010a). However, unlike in the epipelagic zone, their biomass here decreased in the warm season but increased in the cold period. This is probably due to the cooling of the surface water in winter when a part of the jellyfish population descends into greater depths and in spring migrate back into the epipelagic zone.

Jellyfish biomass varied greatly from year to year. In the fall, high jellyfish biomass occurred for several years in the 1990s (1994, 1998, 1999) and again in 2009–2012 (Fig. 4.6.2a). During 2000–2008, jellyfish biomass was at a relatively low level which might be accounted for by the changes in the oceanographic conditions observed in 1998–2001. Based on near-bottom water temperature and ice cover values, this period was the coldest recorded over the last several decades (Zavolokin, 2010a). During spring, jellyfish dynamics showed a more biennial fluctuation, and were much more numerous in odd years (2005, 2007, 2009).

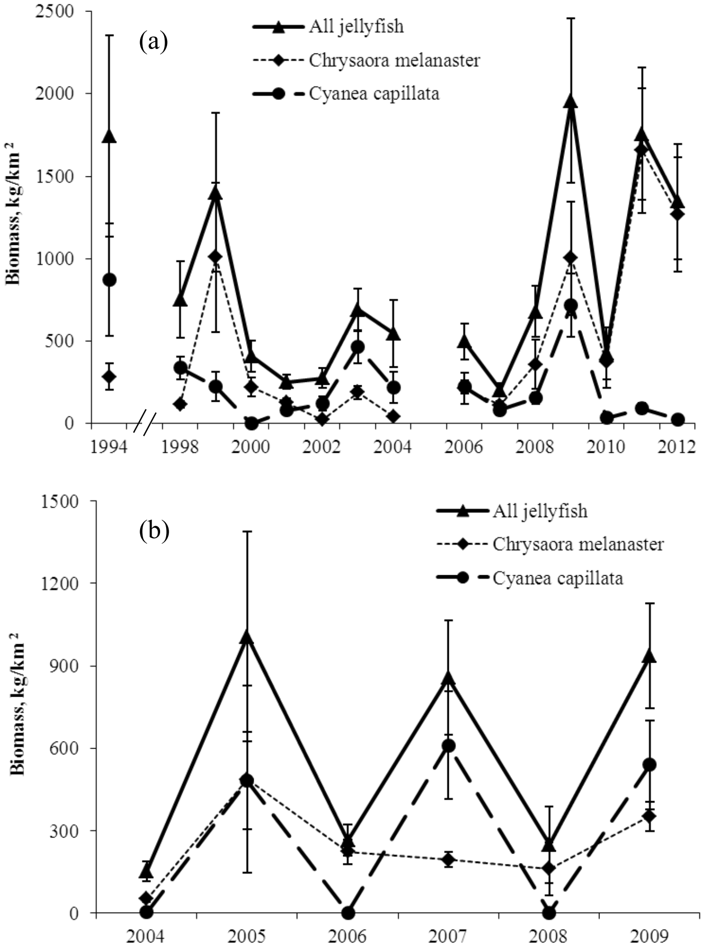


Fig. 4.6.2 Changes in jellyfish biomass (kg km^{-2}) in the northern Okhotsk Sea in fall (a) and spring (b). Standard errors of the means are shown for each value.

Hydromedusae *A. digitale* was the most abundant species of smaller jellyfish caught by a plankton net. Seasonally, the fluctuations in their biomass were relatively small (Table 4.6.3) in comparison with the larger jellyfish. In the northern Okhotsk Sea, their biomass varied from 1.6 mg m^{-3} in fall to 6.1 mg m^{-3} in summer. In the southern part, it biomass varied from 0.9 mg m^{-3} in winter to 2.3 mg m^{-3} in spring.

Table 4.6.3 Seasonal changes in *Aglantha digitale* biomass (mg m^{-3}) in the Okhotsk Sea from 1991–2012. Data are mean biomass ± SE.

Region	Spring	Summer	Fall	Winter
North	2.2 ± 0.1	6.1 ± 1.4	1.6 ± 0.2	2.5 ± 0.4
South	2.3 ± 0.2	1.1 ± 0.1	1.3 ± 0.1	0.9 ± 0.2

The biomass of *A. digitale* tended to change tenfold from year to year (Fig. 4.6.3). In spring, they were at their highest level in 2009. In summer, blooms of *A. digitale* occurred in 1996. From 1998–2001, the biomass of *A. digitale* remained low both in spring and summer, which may have been caused by the abnormally cold conditions occurring in those years.

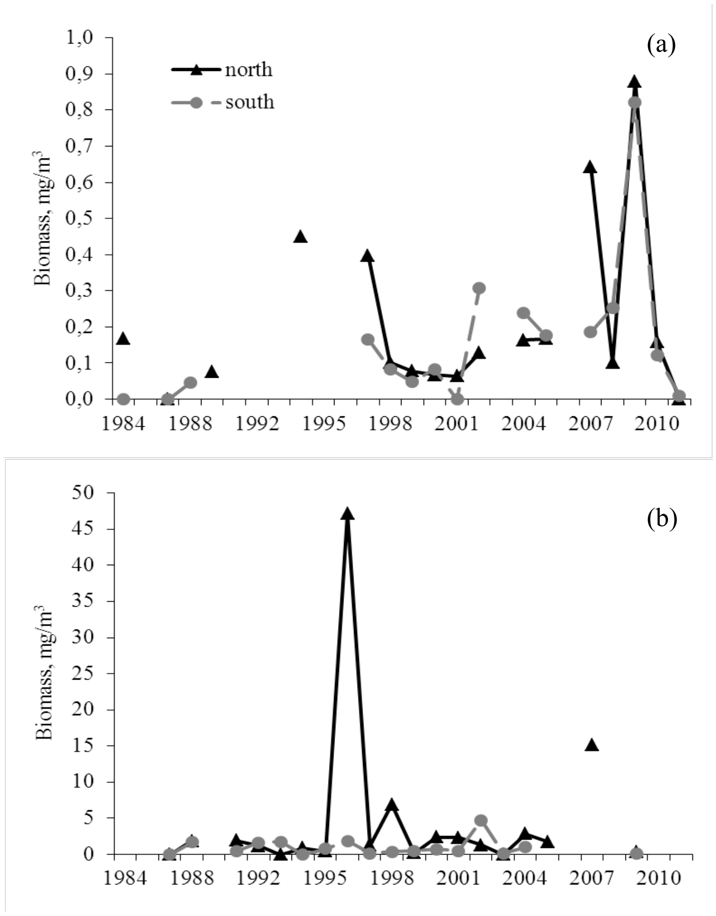


Fig. 4.6.3 Changes in *Aglantha digitale* biomass (mg m^{-3}) in the northern and southern Okhotsk Sea in (a) spring and (b) summer. Note differences in scale.

4.7 Western North Pacific Ocean

Alexander Zavolokin

Pacific Scientific and Research Fisheries Center (TINRO-Center), Vladivostok, Russia

This section is based on the collections made during 32 epipelagic surveys conducted by TINRO-Center in the Western North Pacific Ocean from 1991–2012. About 2,000 trawls were made during this period, with the majority of them (56%) occurring in summer. Jellyfish were caught using pelagic trawls with a vertical opening of 30–55 m and a horizontal opening of 28–49 m, with a small-mesh (1 cm) liner insertion at the codend.

Over the period 1991–2012, 12 species of jellyfish were recorded for the Western North Pacific Ocean, with 8 species belonging to the class Scyphozoa (*Atolla wyvillei*, *Aurelia aurita* s.l., *A. labiata*, *A. limbata*, *Chrysaora melanaster*, *Cyanea capillata*, *Periphylla periphylla*, *Phacellophora camtschatica*) and 4 species belonging to the class Hydrozoa (*Aequorea* sp., *Calycopsis nematophora*, *Ptychogena lactea*, *Tima sachalinensis*). Two species of ctenophores (*Beroe* sp., *Hormiphora cucumis*), five species of salps (*Cyclosalpa* sp., *Helicosalpa* sp., *Salpa aspera*, *S. fusiformis*, *S. maxima*), one species of pyrosomes (*Pyrosoma atlanticum*), and one unidentified species of siphonophores were caught. Hydromedusae and Scyphomedusae were caught in the trawl catches throughout the year, whereas ctenophores, salps, pyrosomes and siphonophores were observed usually in winter and spring when they were likely the most abundant.

Jellyfish were widespread in the Western North Pacific Ocean (Figs. 4.7.1 and 4.7.2). They were found in trawl catches from all areas except in the Subarctic frontal zone. In summer and fall, jellyfish had the highest concentrations in the Pacific waters of eastern Kamchatka (Fig. 4.7.1a), and Commander Islands and Aleutian Islands (not shown). To the south, their biomass decreased sharply. This distribution pattern was similar for all dominant species of large jellyfish: *C. melanaster*, *P. camtschatica* and *Aequorea* sp. (Fig. 4.7.1b,c,d) as well as the small Hydromedusae *Aglantha digitale* (Volkov, 2007). Jellyfish biomass in the study area was likely related to their inflow with currents from the Bering Sea and shelf of the Commander and Aleutian islands, where they were much more abundant in comparison with deep-water regions of the North Pacific. This was especially obvious for *C. melanaster* which had very high biomass in the Bering Sea during this period (Brodeur *et al*., 2008b). In winter and spring, jellyfish biomass greatly decreased and their distributions became less aggregated (Fig. 4.7.2), but the general pattern of distribution was similar to summer and fall. Most of jellyfish concentrated along eastern Kamchatka and the Kuril Islands, and were less abundant offshore.

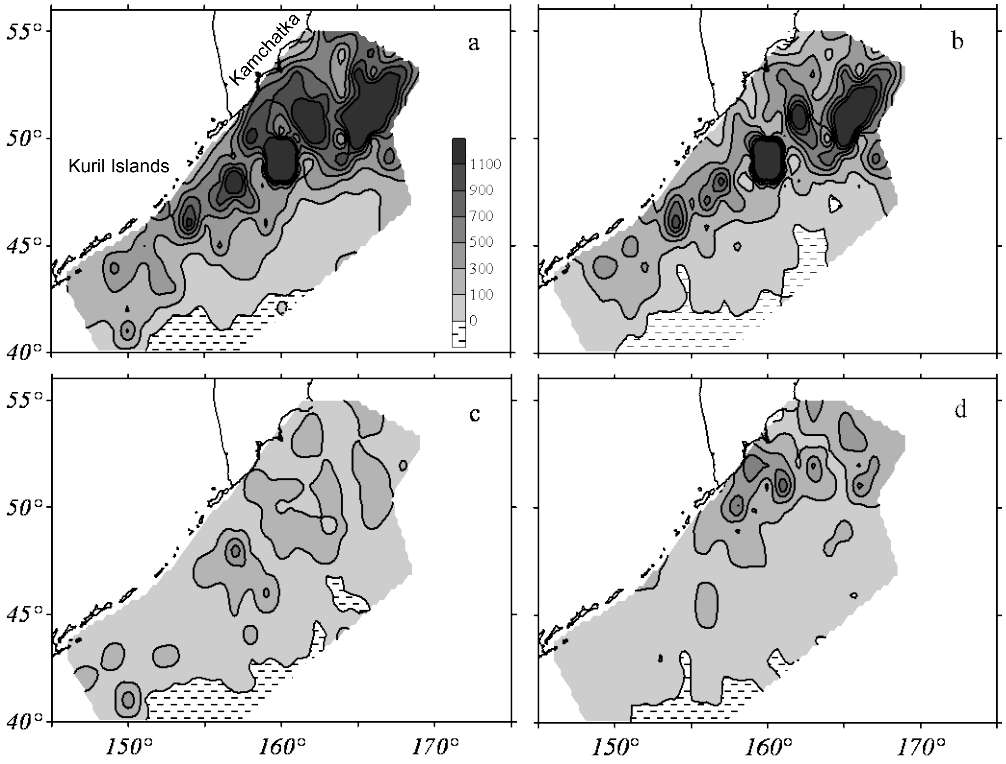


Fig. 4.7.1 Distribution of jellyfish (kg km^{-2}) in the Western North Pacific Ocean in summer and fall, 1991–2011 for (a) all jellyfish, (b) *Chrysaora melanaster*, (c) *Phacellophora camtschatica* and (d) *Aequorea* sp.

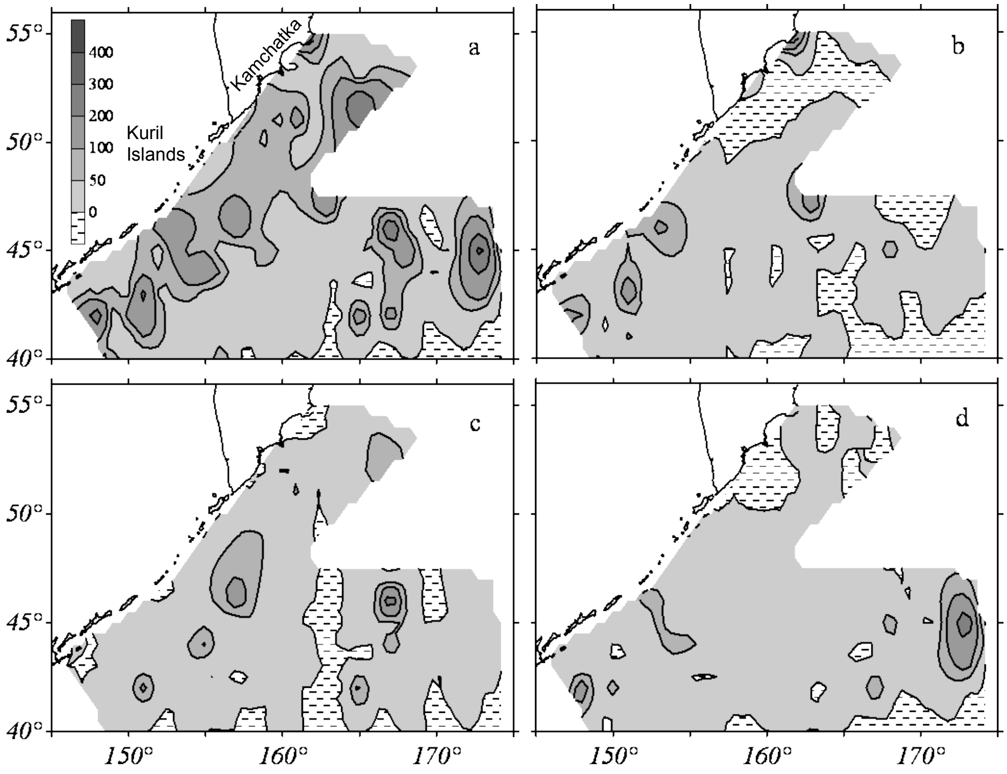


Fig. 4.7.2 Distribution of jellyfish (kg km^{-2}) in the Western North Pacific Ocean in winter and spring, 1991–2011 for (a) all jellyfish, (b) *Chrysaora melanaster*, (c) *Phacellophora camtschatica* and (d) *Aequorea* sp.

Decreases in jellyfish biomass were accompanied by changes in their vertical distribution. In summer, most jellyfish generally inhabited the upper 50-m layer, whereas they migrated into deeper layers in spring (Zavolokin, 2010c).

Seasonally, jellyfish biomass varied greatly. They had the highest biomass in the fall (Table 4.7.1). This seasonal pattern was typically found for all jellyfish species but *C. melanaster* which had the highest concentrations at the end of summer. It is noteworthy that similar seasonal changes of *C. melanaster* biomass were found in other regions of the North Pacific (Zavolokin, 2010b, 2011). In winter and spring biomass and abundance of large jellyfish (*C. melanaster*, *C. capillata*, *P. periphylla*, *P. camtschatica*, *Aequorea* sp.) decreased tenfold. In contrast, biomass and abundance of small jellyfish (*C. nematophora, P. lactea, A. digitale*) as well as ctenophores, salps, pyrosomes and siphonophores stayed at high levels during the cold seasons.

Table 4.7.1 Seasonal changes in jellyfish biomass (kg km$^{-2)}$ in the epipelagic layer of the Western North Pacific Ocean. Data are mean biomass ± SE).

Taxon	**Spring**	**Summer**	**Fall**	**Winter**
Scyphozoa	64.2 ± 17.0	441.4 ± 62.9	480.7 ± 49.8	56.7 ± 9.6
Chrysaora melanaster	18.0 ± 5.4	351.8 ± 62.1	329.7 ± 47.4	34.7 ± 9.2
Phacellophora camtschatica	19.5 ± 13.7	74.8 ± 6.8	77.7 ± 9.5	10.0 ± 2.3
Hydrozoa	28.2 ± 9.3	64.2 ± 7.2	266.6 ± 45.9	7.7 ± 1.6
Aequorea sp.	26.8 ± 9.3	63.3 ± 7.2	265.2 ± 45.9	6.4 ± 1.5
Calycopsis nematophora	0.3 ± 0.1	0.9 ± 0.1	1.4 ± 0.3	1.3 ± 0.6
Number of stations	68	878	276	116

Chrysaora melanaster dominated trawl catches in the Western North Pacific Ocean (Table 4.7.1), comprising 44 to 70% and 19 to 45% of the total jellyfish biomass in the warm and cold seasons, respectively. *Aequorea* sp. was the next dominant species, comprising from 10 to 35 % of the overall jellyfish biomass. In terms of abundance, *Aequorea* sp. and *C. melanaster* were the prevalent species in trawl catches. These two species comprised 47 to 87% of the total jellyfish abundance.

Biomass of jellyfish varied greatly from year to year. Figure 4.7.3 shows that jellyfish biomass during the summer changed tenfold, from about 80 kg km^{-2} in 2011 to 900 kg km^{-2} in 1993. The interannual dynamics between different species did not show any similarities and biomass fluctuated nonsynchronously resulting in changes of dominant species (*C. melanaster*, *P. camtschatica* and *Aequorea* sp.) from year to year.

In winter and spring, a significant part of the trawl catches consisted of ctenophores, salps, pyrosomes and siphonophores (Fig. 4.7.4). In 2011, the biomass of these groups was even higher than total medusae biomass. Considering the low catchability of ctenophores, salps, pyrosomes and siphonophores in this sampling gear, their biomass is likely to be much higher. In the cold seasons, the species composition and magnitude of biomass fluctuations of jellyfish were similar to those in the summer. *C. melanaster*, *P. camtschatica* and *Aequorea* sp. were the dominant species in terms of biomass.

Fig. 4.7.3 Changes in jellyfish biomass (kg km^{-2}) in the Western North Pacific Ocean from 1993– 2012 for (1) all jellyfish, (2) *Chrysaora melanaster*, (3) *Phacellophora camtschatica* and (4) *Aequorea* sp.

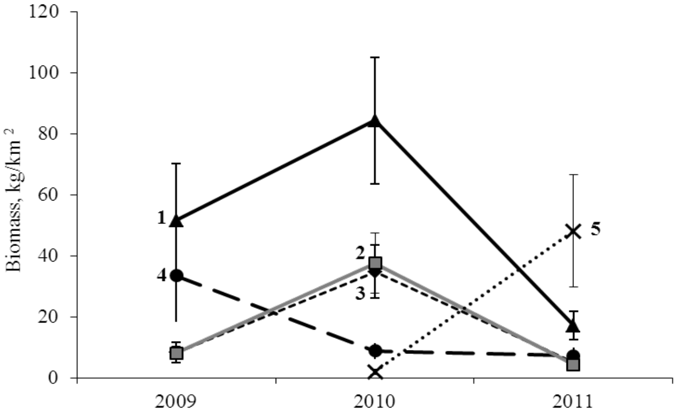


Fig. 4.7.4 Changes in biomass (kg km^{-2}) of gelatinous zooplankton in the Western North Pacific Ocean in February–April for (1) all jellyfish, (2) *Aequorea* sp., (3) *Chrysaora melanaster*, (4) *Phacellophora camtschatica* and (5) ctenophores, siphonophores, salps, and pyrosomes.

The total biomass of large jellyfish was similar to the biomass of the dominant small Hydromedusae *A. digitale*, based on collections from a Jedy plankton net (Table 4.7.2). Taking into account other small jellyfish as well as ctenophores, salps, pyrosomes and siphonophores, the overall biomass of gelatinous zooplankton in the Western North Pacific Ocean could possibly be 2 to 3 times higher than estimates based on the data of trawl catches.

Table 4.7.2 Biomass (mg m^{-3}) of large jellyfish (from trawl catches) and the small Hydromedusae *Aglantha digitale* (from Juday plankton hauls) in the Western North Pacific Ocean. Plankton data from Volkov (2007).

Jellyfish (gear)	Spring	Summer	Fall	Winter
Large jellyfish (pelagic trawl)	1.5	13.3	22.2	1.3
Aglantha digitale (plankton net)	12.3	7.3	8.6	1.4

4.8 Japanese Coast

Shin-ichi Uye[1], Haruto Ishii[2] and Masaya Toyakawa[3]

[1] Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Japan
[2] Tokyo University of Marine Science and Technology, Tokyo, Japan
[3] Seikai National Fisheries Research Institute, Nagasaki, Japan

4.8.1 Introduction

Because of various ecosystems ranging from the sub-boreal to tropic zone and from shallow to hadal depth, Japanese waters constitute one of the major hotspots in marine biodiversity (Fujikura *et al*., 2010), and harbor at least 500 species in the class Hydrozoa (excluding orders devoid of the medusa stage and freshwater species), 33 species in Scyphozoa, and 4 species in Cubozoa, in addition to 28 species in the phylum Ctenophora (Union of Japanese Societies for Systematic Biology, 2003). Among them, the moon jellyfish *Aurelia aurita* s.l., which is designated as *Aurelia* sp. 1 from DNA sequence analysis (Dawson and Jacobs, 2001; Endo *et al*., 2011), is the most common because of the seasonal aggregation of its medusae, and has been recorded since ancient times. Kojiki, the oldest Japanese history book, published in 712 AD, related that the beginning of the Japanese islands were like aggregated medusae (most likely *A. aurita* s.l.) on the sea surface!

Ecological studies of scyphozoan jellyfish in Japan were pioneered by Dr. Toru Yasuda (1938–2012), who initiated an intensive survey on *A. aurita* s.l. in Urazoko Bay, a small inlet in Fukui Prefecture, central Japan, in the 1960s (Yasuda, 1969, 1983). Around this time, a noticeable increase in the *A. aurita* s.l. population took place in Tokyo Bay; aggregated medusae clogged the ingress of cooling water of power plants, which caused blackouts in the Tokyo metropolitan area (Kuwabara *et al*., 1969). However, jellyfish were largely neglected in planktology or fishery science until around 2000, when problematic blooms of not only *A. aurita* s.l. but also the giant jellyfish *Nemopilema nomopilema* became prominent in Japanese coastal waters. Since then, more scientists began to study jellyfish, and much scientific knowledge has been accumulated. In particular, two major national and international projects, *i.e*., Studies on Prediction and Control of Jellyfish Outbreaks (STOPJELLY) from 2007 to 2012, and the Japan-China-Korea International Jellyfish Project from 2006 to present, both sponsored by the Ministry of Agriculture, Forestry and Fisheries of Japan, have contributed significantly to the advancement of jellyfish studies. This section gives brief overviews of studies conducted in three coastal waters: the Inland Sea of Japan (Seto Inland Sea), Tokyo Bay, and Ise Bay and Mikawa Bay, where *A. aurita* s.l. is the major bloom-forming species, and in the Sea of Japan, a part of the East Asian Marginal Seas, where massive outbreaks of *N. nomurai* have occurred repeatedly in the last two decades (Fig. 4.8.1).

4.8.2 Inland Sea of Japan (Seto Inland Sea)

Long-term variations in the occurrence of jellyfish

The Inland Sea of Japan, a narrow coastal sea (east–west length: approximately 450 km, north–south width: 15–50 km, area: 23,203 km^2, average depth: 38 m) is enclosed by Honshu, Shikoku and Kyushu (Fig. 4.8.1). It has long been famous for its beautiful landscape including approximately 1,000 islands, and hence was designated as Japan's first national park in 1934. It is also a productive fisheries ground;

the annual fish catch per unit area (average in the early 1990s: 20.5 tons km^{-2} yr^{-1}) is one of the world's highest value fisheries areas (Takeoka, 1997). Due to the slow replacement rate of the water within this semi-enclosed sea (average residence time approximately 15 months, Takeoka, 1984) and large human population (34 million) along its coast, the anthropogenic impact on this sea is considered significant. Particularly in the 1960s and 1970s, pollution by industrial as well as by household wastes increased eutrophication of the sea and gave rise to frequent occurrences of red tides, including some 300 incidents in 1976 (Fisheries Agency of Japan). In 1973, a promulgation of laws resulted in a permanent Law Concerning Special Measures for Conservation of the Environment of the Seto Inland Sea (Seto Inland Sea Law) in 1978 leading to intensive measures to decrease the load of pollutants from the land so that the red tides actually decreased to about 100 incidents in 1990, and thereafter they have remained stable.

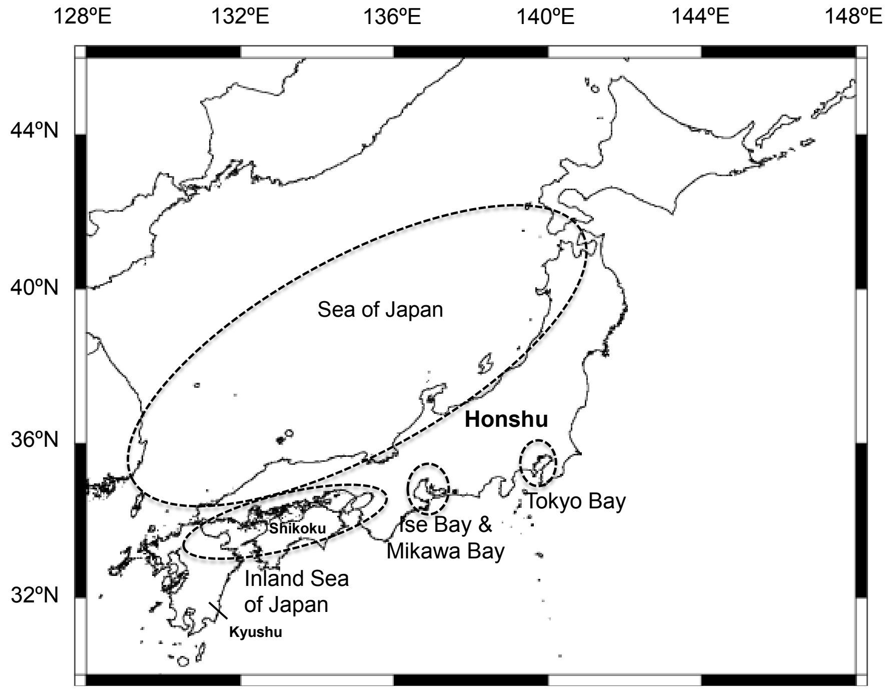


Fig. 4.8.1 Map of Japan showing locations of the Inland Sea of Japan (Seto Inland Sea), Ise Bay, Mikawa Bay, Tokyo Bay and the Sea of Japan, where jellyfish blooms are problematic.

In the Inland Sea of Japan, *Aurelia aurita* s.l. is always the most abundant and most problematic jellyfish species. A remarkable increase in inquiries from local fishermen asking about useful methods to lessen the clogging damage of their nets by *A. aurita* s.l. in the 1990s made us realize the importance of studying jellyfish. In 2000, a hitherto-unreported large-scale bloom of *A. aurita* s.l. occurred, with an estimated biomass of approximately 9.4 × 10^4 tons wet weight (WW) extending along approximately 100 km of the coastline of the Uwa Sea, southwestern Shikoku (Uye *et al.*, 2003). In 2002, an extensive survey of fishermen was conducted regarding the socio-economic impact of jellyfish to their fisheries (Uye and Ueta, 2004). Of a total of 1,152 respondents with more than 20 years of experience as fishermen, 65% believed that the *A. aurita* s.l. population had increased in the last 20 years, *i.e.*, since the early 1980s, and most noticeably in the last 10 years, *i.e.*, since the early 1990s (Fig. 4.8.2). Most fishermen also noted a gradual extended period of occurrence (*i.e.*, earlier appearance and later disappearance) of medusae over the last 20 years and, in extreme cases, the occurrence of over-wintering medusae. They reported that other jellyfish species, such as *Chysaora pacifica, Cyanea nozakii* and *Bolinopsis mikado* also seasonally aggregated to cause a nuisance to the fishery. Although no systematic surveys have been conducted since 2002, all available information from fishermen and news media suggests that the *A. aurita* s.l. biomass remains almost the same as around 2000.

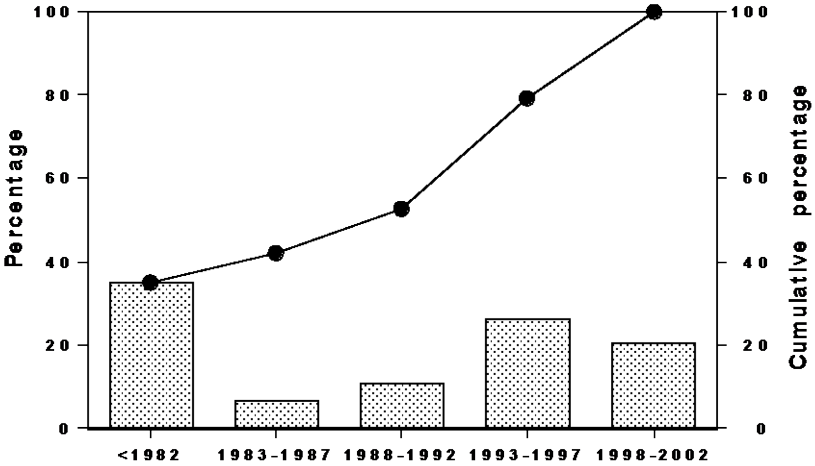


Fig. 4.8.2 Polling results of fishermen showing the periods (<1982, 1983–1987, 1988–1992, 1993–1997 and 1998–2002) when *Aurelia aurita* s.l. began to increase in the Inland Sea of Japan; <1982 means that the occurrence of *A. aurita* was the same before 1982 as at present. Columns indicate percentage of the respondents for the respective periods. Line indicates cumulative percentage through time (from Uye and Ueda, 2004).

The undersides of marine structures, such as docks, floating piers and buoys provide suitable habitat for *A. aurita* s.l. polyp colonies to attach (Watanabe and Ishii, 2001; Miyake *et al*., 2002; Duarte *et al*., 2012). Makabe *et al*. (2014) demonstrated the attachment of *A. aurita* s.l. polyps and their colony development on the undersurface of a floating pier (48 m × 6 m) newly installed in a fishing port in Hiroshima Bay. The polyps began to colonize the undersurface of the pier 4 months after the installation, and then reached a peak density (4.5 polyps cm^{-2}) a month later. The polyp population on the pier released a total of 25 million ephyrae a year after the installation, demonstrating that marine structures such as floating piers add new polyp substrates, which give rise to more ephyrae, thus increasing medusae blooms.

4.8.3 Tokyo Bay

Tokyo Bay (area: 1380 km^2, average depth: 38.6 m) is one of the most eutrophic bays in Japan because of the location of several big cities, such as Tokyo, Yokohama and Chiba along its waterfront (Fig. 4.8.1). From the 1960s to the 1970s, Tokyo Bay was the site of extensive land reclamation, with a total area of 250 km^2, about 20% of the original Tokyo Bay sea area, of the reclaimed land converted for industrial use. Although there have been no significant long-term changes in temperature and salinity since the 1950s, the increase in eutrophication, as represented by the increase in dissolved inorganic nitrogen (N) and phosphorus (P), was significant (Nomura, 1994). For example, total dissolved inorganic nitrogen (*i.e.*, sum of NO_3^-, NO_2^- and NH_4^+) concentration was lower than 25 µg-at l^{-1} before 1965 but increased to more than 50 µg-at l^{-1} by 1990. Dissolved inorganic phosphorus (PO_4^-) concentration was less than

0.3 μg-at l^{-1} until 1965 but it increased to approximately 1 μg-at l^{-1} by 1990. These concentrations have remained relatively stable since 1990. In association with such a rapid increase in nutrient loads, red tide phytoplankton blooms have chronically taken place, and the annual average chlorophyll *a* concentration in the surface water peaked around 50 μg l^{-1} during the period from 1969 to 1980. Since then, however, there has been no significant decreasing trend in chlorophyll *a* concentration. Accordingly, benthic hypoxia became significant in the 1980s, when the dissolved oxygen concentration near the sea bottom decreased to 0–1 mg O_2 l^{-1} in summer.

Long-term and seasonal variations in the occurrence of Aurelia aurita s.l.

The seasonal life cycle of *A. aurita* s.l. in Tokyo Bay is basically similar to that in many other Japanese coastal waters. The strobilation of benthic polyps takes place from December to April, followed by the release of ephyrae into the plankton, which grow to adult medusae by early summer (Sugiura, 1980; Ishii *et al*., 1995, 2004; Nomura and Ishimaru, 1998; Toyokawa *et al*., 2000; Watanabe and Ishii, 2001). Then, the mature medusae sexually reproduce planula larvae, which are planktonic before settlement onto hard substrates (Ishii *et al*., 2008). Although most medusae die by October, they can sometimes overwinter to the next spring, leading to the occurrence of medusae throughout the year (Omori *et al*., 1995).

No data were available on the abundance of *A. aurita* s.l. before the 1960s; the occurrence of dense aggregations of medusae were reported for the first time in 1966 and 1967 in the innermost part of Tokyo Bay, *i.e*., the Chiba-Ichihara area when these medusae affected the operation of power plants on the coast (Kuwabara *et al*., 1969). The environmental and ecosystem conditions created in the 1960s and 1970s during rapid human modification of the coastal geomorphology, and subsequent eutrophication, might have been favorable for the increase of the *A. aurita* s.l. population.

As planulae of *A. aurita* s.l. never settle directly on bottom sediments, and the polyps are often found on artificial structures such as vertical concrete walls and floating piers (Ishii and Katsukoshi, 2010), the increase in land reclamation and artificial construction may lead to the expansion of polyp habitat. Polyps of *A. aurita* s.l. are much more tolerant of low dissolved oxygen concentrations than other sessile organisms, such as mussels, that compete for attachment space with the polyps. Indeed, the polyp colonies are often found near the bottom hypoxic layer where other sessile organisms are scarce (Ishii *et al*., 2008; Ishii and Katsukoshi, 2010), suggesting the monopolization by the polyps under hypoxic conditions. Along with eutrophication, the zooplankton community composition, particularly that of copepods, changed. The copepods were predominately calanoid species, *e.g*., *Acartia omorii* and *Paracalanus purvus* s.l., before the 1950s (Yamazi, 1955), but were largely monopolized by the small cyclopoid *Oithona davisae* after the 1960s (Nagasawa and Marumo, 1984). It is speculated that *O. davisae* may be too small to be consumed by many fish species, which tend to visually select larger calanoids, but may be a preferable food item for *A. aurita* s.l., which can capture relatively small prey using nematocyst-laden tentacles. Consequently, the annual fish catch peaked at ~140,000 tons WW in the early 1960s, and then declined to <30,000 tons WW by 1990 (Kakino *et al*., 2011).

Periodic monitoring conducted in central Tokyo Bay from 1981 to 1996 did not show any increasing trend in *A. aurita* s.l. population size, but rather it remained relatively constant (Nomura and Ishimaru, 1998). In the following period from 1998 to 2012, the annual average density of *A. aurita* s.l. in the innermost part of Tokyo Bay fluctuated markedly year by year (Fig. 4.8.3, Ishii, unpubl.). Hence, it is speculated that *A. aurita* s.l. abundance might have attained some maximum level by the 1970s, thereafter showing prominent interannual variations. Interviews with local fishermen and marine workers (*e.g*., barge captains) also indicate that there has not been a significant increase in *A. aurita* s.l. in recent decades (Ishii, pers. comm.).

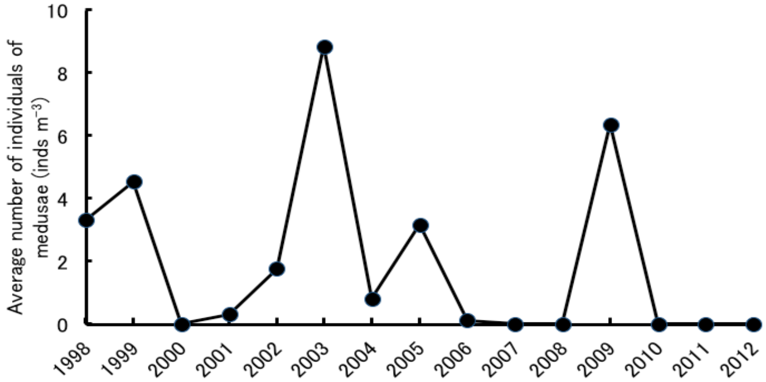


Fig. 4.8.3 Long-term variations in annual average abundance of *Aurelia aurita* s.l. medusae in the innermost part of Tokyo Bay. Surveys conducted by the T/V *Hiyodori* of the Tokyo University of Marine Science and Technology (from Ishii, unpubl.).

Occurrence of other jellyfish species

Chrysaora pacifica is the second most important scyphozoan species in Tokyo Bay, and the abundance of this species may have increased since 1990 according to monitoring surveys conducted in central Tokyo Bay from 1981 to 1996 (Nomura and Ishimaru, 1998). Compared to *A. aurita* s.l., the geographical distribution of *C. pacifica* is confined to the offshore, deeper area of Tokyo Bay (Ishii, unpubl. data). The medusa stage of *C. pacifica* begins to appear in February, slightly earlier than *A. aurita* s.l., with the medusae dying off by August (Nomura and Ishimaru, 1998). Other jellyfish species, such as the hydrozoan *Spirocodon saltator* occur mainly from February to April, the scyphozoan *Pelagia noctiluca* in October, and the cubozoan *Carybdea rastoni* from August to October (Nomura and Ishimaru, 1998). In addition, the ctenophore *Bolinopsis mikado* occurs in dense concentrations in summer and autumn seasons (Kasuya *et al*., 2000).

4.8.4 Ise Bay and Mikawa Bay

Ise Bay and adjacent Mikawa Bay (area and average depth: 1,738 km^2 and 19.5 m, and 604 km^2 and 9.2 m, respectively) are located midway along Honshu (Fig. 4.8.1). Eutrophication reached high levels in the 1970s as evidenced by the year-to-year decrease in water transparency (*i.e*., Secchi disk depth), increase in the concentration of macronutrients (*i.e*., nitrogen and phosphorus), and increasing frequency of red tides (Saijo, 1984; Suzuki *et al*., 2011; Ishida and Aoyama, 2012). In addition, the loss of tidal flats and shallow coastal areas through land reclamation and the occurrences of benthic hypoxia were most prominent in the 1970s (Suzuki *et al*., 2011). From 1956 to 1985, a total area of 45.3 km^2 and 34.6 km^2 was reclaimed in Ise Bay and Mikawa Bay, respectively (The Chubu Regional Bureau, 2008). However, due to legal regulations concerning nitrogen and phosphorus loads from the land to the sea, eutrophication began to decline in the late 1980s (Ishida and Aoyama, 2012). Annual fish catch in Mikawa Bay has been relatively stable (*i.e*., ~ 6×10^4 tons WW over the last 50 years) except for high values of $>8 \times 10^4$ tons WW from the late 1970s to the late 1980s, when the Japanese sardine was abundant (Ishida and Aoyama, 2012).

Occurrence of jellyfish

Aurelia aurita s.l. is the most dominant scyphozoan species in Ise Bay and Mikawa Bay. The major source of *A. aurita* s.l. medusae in Mikawa Bay is from several fishing ports on Himaka and Shino islands located in the mouth of the bay (Fig. 4.8.4). In these ports, enormous numbers of polyp colonies attach on the underside of floating piers and old boats, releasing planktonic ephyrae (Hamada, 2003; Toyokawa *et al*., 2011). Strobilation occurs from December to May, most prominently in December (Toyokawa *et al*., unpubl. data). In Mikawa Bay, recruitment of small medusae into the population was observed in March in the western part of the bay, or near the bay mouth (Aoki *et al*., 2012a). The geographical distribution of medusae shifts to the eastern part of the bay toward summer (Aoki *et al*., 2012a), being affected by intrusions of seawater from offshore and the diel vertical migration of the medusae (Aoki *et al*., 2012b). The medusae are most abundant from May through July (Shirokiya *et al*., unpubl. data).

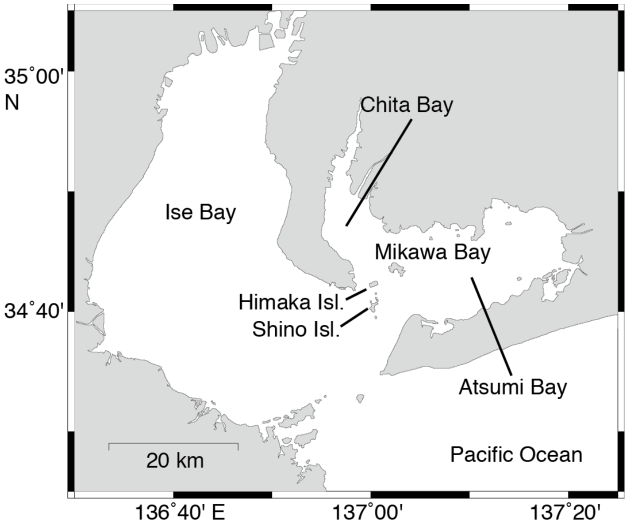


Fig. 4.8.4 Map of Ise Bay and Mikawa Bay showing locations of Himaka Island and Shino Island, where dense *Aurelia aurita* s.l. polyp colonies inhabit fishing ports on the islands (from Tokokawa *et al*., 2011).

Following *A. aurita* s.l.*, C. pacifica* is the next most important species, occurring primarily as medusae from January to June (Yamada *et al*., 2008), but no data are available regarding its long-term trends or geographical distributions. Although several Hydromedusae species, *i.e*., *Aequorea coerulescens*, *Liriope tetraphylla* and *Muggiaea atlantica* and a ctenophore species *B. mikado* are occasionally abundant (Toyokawa *et al*., unpubl. data), they have never been reported to cause problems in fisheries and power plant operations.

4.8.5 Sea of Japan

The Sea of Japan is a marginal sea of the western Pacific enclosed by the Asian continent, the Japanese Archipelago and Sakhalin Island, with area of 9.78×10^5 km^2 and maximum and average depths of 3,742 and 1,750 m, respectively (Fig. 4.8.1). Two major currents circulate in a counterclockwise direction: the warm Tsushima Current, which originates in the East China Sea and flows along the Japanese coast to the north, and the cold Liman Current, which starts in the northern Sea of Japan and flows along the Asian coast to the south. The Tsushima Current is responsible for the transportation of the giant jellyfish *Nemopilema nomurai* (Class Scyphozoa), which attains the maximum bell diameter and body weight of approximately 2 m and 200 kg, respectively (Shimomura, 1959; Yasuda, 2007) and is endemic to the East Asian Marginal Seas, including the Bohai Sea, Yellow Sea, East China Sea and the Sea of Japan.

Long-term variations in the occurrence of jellyfish

In the Sea of Japan, a prominent bloom of *N. nomurai* was first recorded in 1920 (Kishinouye, 1922), followed by two more records, in 1958 (Shimomura, 1959) and 1995 (Yasuda, 2007), a rate of about one record per 40 years in the 20th century. In the present century there has been a remarkable increase in bloom frequency. In 2002, only 7 years after the previous bloom, enormous numbers of *N. nomurai* medusae appeared in Japanese coastal waters, causing severe damage in fisheries. Since then, blooms (*e.g.*, >2,000 medusae entrapped per set net per day) occurred almost annually up to 2009 after which medusae numbers declined (*e.g.*, <100 medusae entrapped per set net per day) up to 2015. In bloom years, massively aggregated *N. nomurai* caused serious problems.

In addition to *N. nomurai*, coastal species such as *A. aurita* s.l. and *C. pacifica* also showed an increase in abundance in recent decades, as local fishermen have often encountered aggregations of these species, causing their fishing nets to burst. The trend of increasing populations of these species is essentially the same as in the major Japanese bays and embayments as described above.

Seasonal and geographical distribution of N. nomurai

The large bay system flanked by the Korean Peninsula and the mainland of China, *i.e.*, the Bohai Sea, Yellow Sea and East China Sea, is the geographical origin of *N. nomurai*. Although the polyps have not yet been found, this area is thought to be the main benthic habitat of this species (Hon *et al*., 1978; Cheng *et al*., 2004; Kawahara *et al*., 2006) because its ephyrae and small (bell diameter: <10 cm) medusae have been collected (Toyokawa *et al*., 2012; Sun *et al*., 2015) and sighted only in this region. The ephyrae are released into the plankton from the benthic polyps during spring to early summer. Many individuals spend their planktonic life as medusae in this area until they die in winter (Zhang *et al*., 2012; Sun *et al*., 2015), and thereby the endemism of this species is maintained. However, the majority of medusae in the southern Yellow Sea and northern East China Sea are expatriated by currents (Fig. 4.8.5). Due to monsoonal rainfall in June and July in temperate East Asia, the Chanjiang (Yangtzu River) low salinity water mass (CLSWM) forms, with its front extending close to Jeju Island, Korea. The young medusae are entrained into this offshore-spreading CLSWM and are then transported northward by the Tsushima Current to the Tsushima Strait between Japan and Korea in July and August (Chang and Isobe, 2003; Reizen and Isobe, 2006; Uye, 2008). The medusae continue to move north along the Sea of Japan coast. In September, the population front passes through the Tsugaru Strait to the Pacific Ocean and is transported south as far as the Boso Peninsula (Fig. 4.8.5). To date, ephyrae and small medusae of *N. nomurai* have never been found in Japanese coastal waters, indicating that the settlement of new polyp populations in Japanese waters remains unsuccessful.

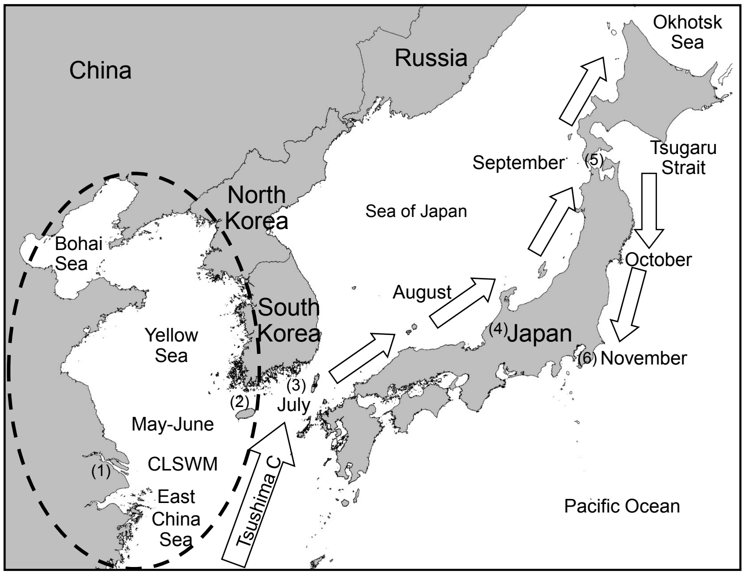


Fig. 4.8.5 Schematic representation of the advective transport of *Nemopilema nomurai* medusae from their seeding and nursery ground (indicated by dashed line) to the Sea of Japan showing major hydrographic features: Changjiang Low Salinity Water Mass (CLSWM) and the Tsushima Current. (1) Changjiang River Estuary, (2) Jeju Island, (3) Tsushima Strait, (4) Fukui Prefecture, (5) Tsugaru Strait, and (6) Boso Peninsula. (modified from Uye, 2008).

Possible causes for blooms of N. nomurai

Recent frequent blooms of *N. nomurai* may possibly be attributed to regional environmental changes rather than to decadal climate change or regime shifts, as suggested for jellyfish blooms in other waters (Lynam *et al.*, 2004; Purcell, 2005; Attrill *et al.*, 2007; Brodeur *et al.*, 2008b). Although it is difficult to specify which factors are really responsible for the increasing *N. nomurai* population, the following factors, which are evident in Chinese coastal waters, are thought to be among the causes (Uye, 2008, 2011).

Over-fishing

The stock sizes of fishes have been declining in the East Asian Marginal Seas over the past several decades. For example, in the Bohai Sea the catch per unit effort declined by approximately 95% from 1959 to 1998 (Tang *et al.*, 2003). In the Yellow Sea, according to Korean fish-catch statistics (National Institute of Fisheries Science (formerly National Fisheries Research and Development Institute), Korea), the annual fish catch declined from about 13 × 10^4 tons WW in the mid-1980s to 5 × 10^4 tons WW in 2004. Furthermore, Japanese fish-catch statistics (Fisheries Agency of Japan) show that the annual fish catches in both the East China Sea and Sea of Japan halved since the 1990s. Such an extreme reduction of fish populations may reduce predation rates on ephyrae and young medusae, and may result in an open ecological niche into which jellyfish populations can fill and expand.

Global warming

Due to recent global warming, the surface temperature in the Yellow Sea increased by 1.7°C from 1976 to 2000 (Lin *et al*., 2005). Our laboratory experiments have demonstrated that the asexual reproduction rate of polyps accelerates by nearly 20% with a similar temperature increase (Uye and Kawahara, unpubl.). Hence, global warming may lead to higher reproduction rates of polyps, as well as to both earlier and longer seasonal occurrences of medusae.

Eutrophication, change in nutrient composition and hypoxia

Because of increased anthropogenic activity in East Asia, particularly in China's eastern coastal zone, nutrient loading from the land is rapidly increasing, as evidenced by dissolved inorganic nitrogen (DIN) and phosphorus (DIP) concentrations in the Changjiang River water (Fig. 4.8.6). At the same time, the concentration of dissolved silica (Si) is decreasing. The input of nitrogen and phosphorus into coastal waters has certainly enhanced phytoplankton production; chlorophyll *a* concentration in the surface water of the Changjiang Plume increased by a factor of 4 from 1984 to 2002 (Wang, 2006), which could be expected to enhance zooplankton production and supply more food to jellyfish. Furthermore, the changing nutrient composition (*e.g*., N/P and Si/N ratios of 35 and 0.85, respectively, in 2002 as compared with the "normal" Redfield ratios of 16 and 1.0, respectively) may have changed the phytoplankton taxonomic composition from diatoms to harmful non-diatom species, including the toxic dinoflagellates *Alexandrium* and *Gymnodinium*, blooms of which increased dramatically in frequency from less than 5 per year in the 1990s to 58 in 2003 (Wang, 2006). Such cultural eutrophication may intensify hypoxia or anoxia in the lower part of the water column as a result of decomposition of excess organic matter, as in the Changjiang outflow area (Chen *et al*., 2007; Wei *et al*., 2007). This condition would result in the reduction of both habitat space and reproduction of most marine species, but not of jellyfish or scyphozoan polyps, which are tolerant of low oxygen concentrations (Condon *et al*., 2001; Shoji *et al*., 2005; Ishii *et al*., 2008; Thein *et al*., 2012).

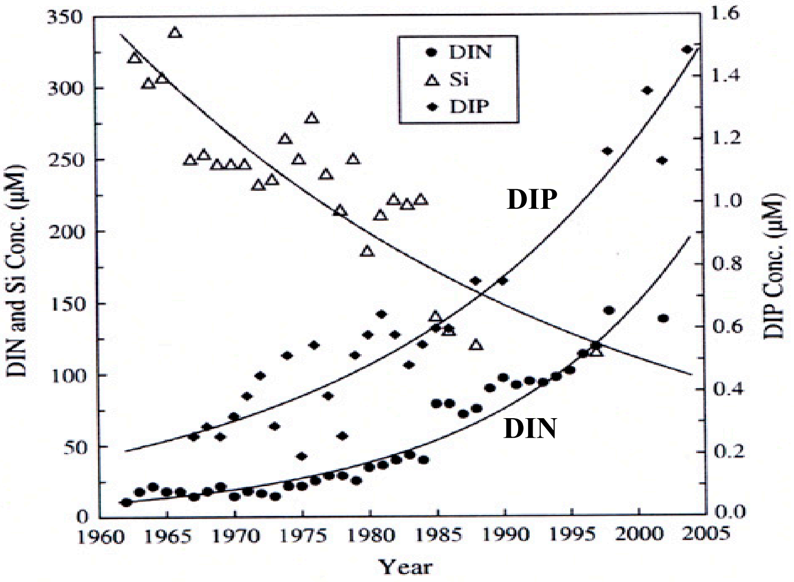


Fig. 4.8.6 Variation in nutrients (DIN = dissolved inorganic nitrogen, DIP = dissolved inorganic phosphorus, Si = dissolved silica) concentrations in Changjiang River water from 1962 to 2002 (from Wang, 2006).

Marine infrastructure and coastal garbage

Marine infrastructures such as harbors, shoreline development, docks, and aquaculture facilities have developed rapidly in China's coastal waters. Although the actual attachment sites of *N. nomurai* polyps have not yet been found, they attach exclusively to hard substrates such as plastic plates and sheets in the laboratory (Kawahara, 2008; Kawahara *et al*., 2006). Hence, marine installations, as well as trash dumped onto the sea floor, may provide new substrates to which polyps can attach, as has been found for the genus *Aurelia* (Miyake *et al*., 2002; Purcell *et al*., 2009; Duarte *et al*., 2012).

4.8.6 Summary

Although the jellyfish blooms have been encountered in Japanese coastal waters since ancient times, they became problematic in the 1960s when the growth of the post-war Japanese economy accelerated at a rapid pace. Because of geographic as well as climatic advantages, many areas of the coastal zone along Tokyo Bay, Ise Bay and the Inland Sea of Japan were utilized for sites of industrial complexes and factories, which consequently resulted in coastal geomorphological changes and eutrophication. In response to such acute environmental changes, population outbreaks of *A. aurita* s.l. started to take place in Tokyo Bay, the most eutrophic bay in Japan, in the 1960s. Population increases of *A. aurita* s.l. have become noticeable in the Inland Sea of Japan since the 1980s, when eutrophication was reduced due to promulgation of the law in 1973 regulating the discharge of nutrients into the marine environment, but other factors such as global warming, increase of anthropogenic polyp habitat, and decrease of fish competitors became more conspicuous. Therefore, the proliferation of *A. aurita* s.l. populations in Japanese coastal waters may be attributed to a spreading and intensified human-perturbed ecosystem. The recurrent population outbreaks of *N. nomurai* in the East Asian Marginal Seas may also be attributed to anthropogenic causes.

4.9 Korean Coast

Changhoon Han[1], Kyoungsoon Shin[2] and Seungshic Yum[2]

[1] National Institute of Fisheries Science, Busan, Korea
[2] Korea Institute of Ocean Science and Technology, Geoje, Korea

4.9.1 Jellyfish species

Thirty-one species of hydrozoan and scyphozoan jellyfishes, including one freshwater species (*Craspedacusta sowerbii*), have been reported in Korean waters (Fig. 4.9.1, Table 4.9.1). However, recent molecular studies have recategorized at least three species – those formerly called *Aurelia aurita* and *Dactylometra quinquecirrha* in Korean waters are now designated as *Aurelia* sp. 1 and *Chrysaora pacifica*, respectively (Ki *et al*., 2008; NFRDI, 2013). The third species, *Carybdea mora*, was not on the list of Animal Systematics, Evolution and Diversity of Korea, and is therefore not shown in Fig. 4.9.1. However, *C. mora* appeared recently, probably due to warming (it is a subtropical species), and caused a number of stinging incidents. It is anticipated that it will be added to the list in the near future. These newly designated species names will be used in this section.

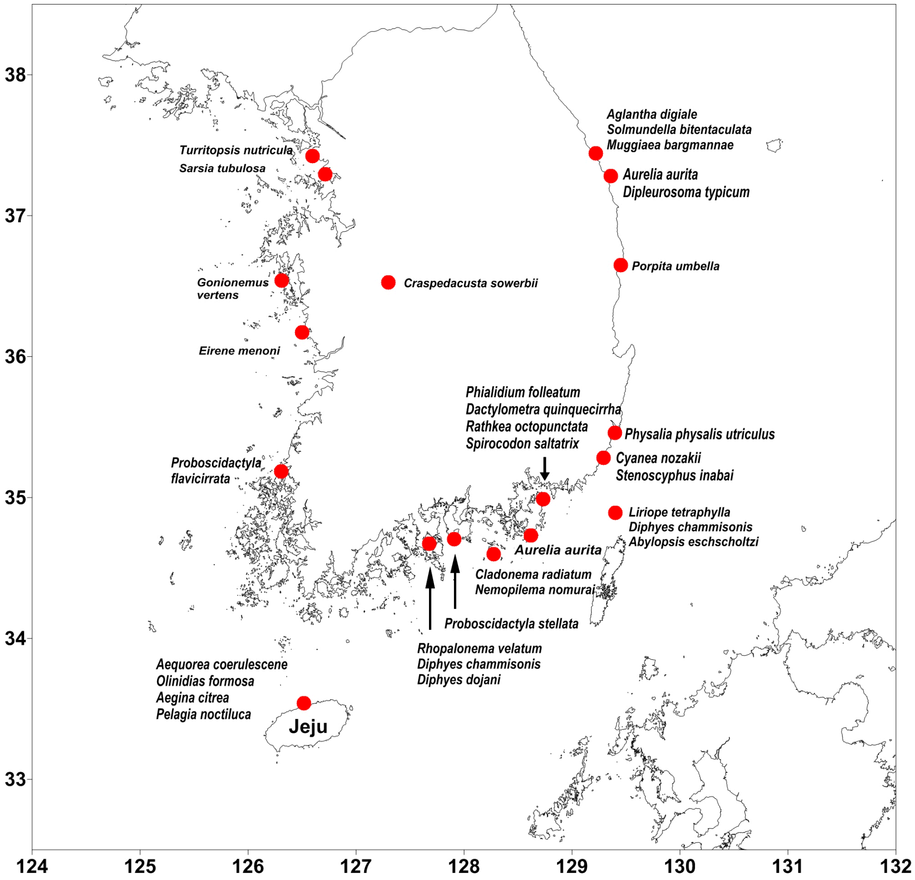


Fig. 4.9.1 Map showing location of occurrence for each of the 31 jellyfish species in Korean waters recorded in Animal Systematics, Evolution and Diversity. *Aurelia aurita* is now referred to as *Aurelia* sp. 1 and *Dactylometra quinquecirrha* as *Chrysaora pacifica*.

Table 4.9.1 List of hydrozoan and scyphozoan jellyfish species in Korean waters reported in Animal Systematics, Evolution and Diversity, ordered according to year referenced in *Animal Systematics, Evolution and Diversity* (see Vols. 12 and 14–22) published by the Korean Society of Systematic Zoology; http://e-ased.org/.

Species	Class-Order	Sampling site
Turritopsis nutricula	Hydrozoa-Anthomedusae	Chakyakto
Cladonema radiatum	Hydrozoa-Anthomedusae	Yokchido
Eirene menoni	Hydrozoa-Leptomedusae	Chunjangdae
Gonionemus vertens	Hydrozoa-Limnomedusae	Anmyondo
*Craspedacusta sowerbii**	Hydrozoa-Limnomedusae	Taechong Dam Reservoir
Rathkea octopunctata	Hydrozoa-Anthomedusae	Geoje Island
Spirocodon saltatrix	Hydrozoa-Anthomedusae	Geoje Island
Dipleurosoma typicum	Hydrozoa-Leptomedusae	Changho Harbour
Stenoscyphus inabai	Scyphozoa-Stauromedusae	Busan (Gijang)
*Aurelia aurita***	Scyphozoa-Semaeostomeae	Samcheok, Geoje Island
Phialidium folleatum	Hydrozoa-Leptomedusae	Geoje Island
Porpita umbella	Hydrozoa-Siphonophora	Hoopo
*Dactylometra quinquecirrha****	Scyphozoa-Semaeostomeae	Geoje Island
Sarsia tubulosa	Hydrozoa-Anthomedusae	Shiwhaho (Kyonggi-do)
Liriope tetraphylla	Hydrozoa-Trachymedusae	Korea Strait
Aequorea coerulescene	Hydrozoa-Leptomedusae	Ulsan
Physalia physalis utriculus	Hydrozoa-Siphonophora	Seogwipo
Proboscidactyla flavicirrata	Hydrozoa-Limnomedusae	Youngkwang
Diphyes dojani	Hydrozoa-Siphonophora	Yeosu
Muggiaea bargmannae	Hydrozoa-Siphonophora	East Sea
Diphyes chammisonis	Hydrozoa-Siphonophora	Korea Strait, Yeosu
Abylopsis eschscholtzi	Hydrozoa-Siphonophora	Korea Strait
Pelagia noctiluca	Scyphozoa-Semaeostomeae	Jeju Harbour, IIgwang
Cyanea nozakii	Scyphozoa-Semaeostomeae	IIgwang
Nemopilema nomurai	Scyphozoa-Rhizostomeae	Yokjido Island, Yeosu
Aegina citrea	Hydorzoa-Narcomedusae	Munseom (Jeju Island)
Solmundella bitentaculata	Hydorzoa-Narcomedusae	East Sea
Proboscidactyla stellata	Hydrozoa-Limnomedusae	Namhae
Olinidias formosa	Hydrozoa-Limnomedusae	Saeseom (Jeju Island)
Aglantha digiale	Hydrozoa-Trachymedusae	Donghae
Rhopalonema velatum	Hydrozoa-Trachymedusae	Yaeyang

* Freshwater species
** Now referred to as *Aurelia* sp. 1
*** Now referred to as *Chrysaora pacifica*

4.9.2 Jellyfish monitoring

There are two ongoing jellyfish monitoring programs in Korea, which are operated by the National Fisheries Research and Development Institute (now known as the National Institute of Fisheries Science, NIFS) (Fig. 4.9.2). One is the Korean Jellyfish Monitoring Network (KoJEM), covering primarily coastal waters. In this monitoring program, a total of 294 fishermen report weekly from May to December to NIFS on the presence/absence of jellyfish at the sea surface or in their fishing nets, which jellyfish species were caught, their location of occurrence, whether they occurred in aggregation or were solitary, and their approximate bell diameter; these data are uploaded to NIFS's homepage (https://www.nifs.go.kr/en/). The other program is the Korean Series of Oceanographic Monitoring Program (KSO), conducted at 207 stations covering primarily offshore waters bimonthly to seasonally by NIFS research vessels *Research 3* and *Research 8*. The KSO is a complex monitoring program including measurements of physical, chemical and biological parameters, in addition to jellyfish sighting surveys, and has been undertaken every year since 2005.

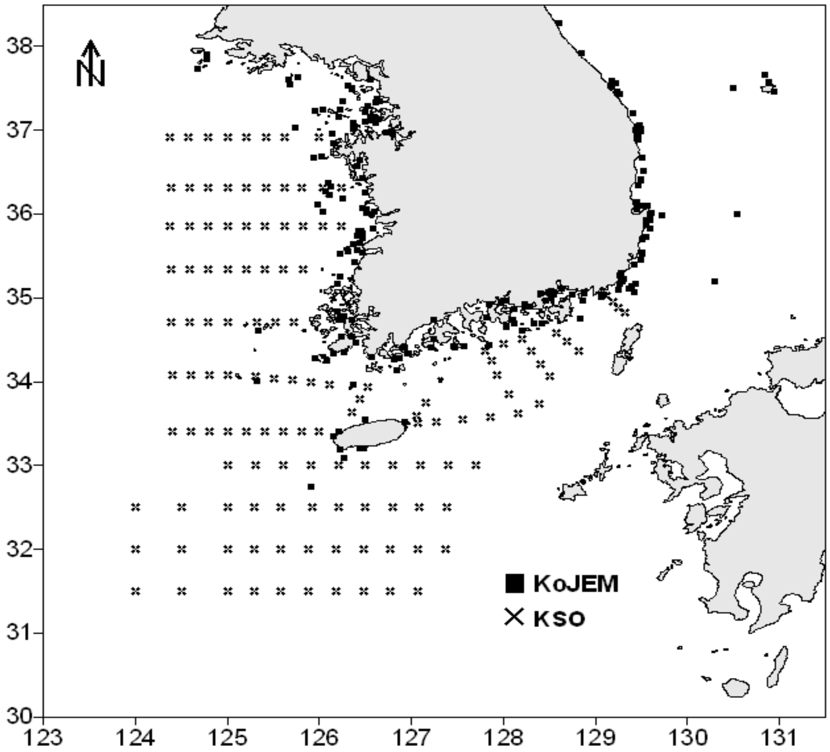


Fig. 4.9.2 Map showing jellyfish monitoring stations in two Korean monitoring programs, the Korean Jellyfish Monitoring Network (KoJEM) and the Korean Series of Oceanographic Monitoring Program (KSO).

Nemopilema nomurai

Korean coastal waters have long been afflicted by outbreaks of the giant jellyfish, *Nemopilema nomurai*, which are carried by currents from the East China Sea and Yellow Sea. Historically, this species was first recorded as Haepalea ("jellyfish" in Korean) in Ja-San-Eo-Bo by Chong in 1814 (Lee, 1970). Since 2003, they have appeared in massive concentrations in Korean waters and have caused serious damage to the fishery industry, stung swimmers, and clogged coastal power plant cooling water intakes (MLTM, 2009). The estimated annual economic losses by this jellyfish alone in fisheries have varied from 68.2 million to 204.6 million USD during the period between 2006 and 2009 (Kim *et al.*, 2012). In 2013, the percentage of beach vacationers who were stung by this species was 11% in 23 beaches examined.

Variability in appearance in coastal waters

Based on KoJEM surveys, annual variations in frequency of appearance (number of stations with appearance/total number of stations) and number of stations where aggregated *N. nomurai* occurred are depicted in Fig. 4.9.3. The frequency of appearance and number of stations with aggregations showed similar patterns, with a significantly positive correlation between them ($r = 0.88$, $p < 0.01$), except in 2008. Judging from these KoJEM data, 2009, 2012, and 2013 are defined as bloom years, and 2010 and 2011 are non-bloom years. The number of stations with appearances of *N. nomurai* also showed remarkable yearly differences between the bloom and non-bloom years (Fig. 4.9.4). The seasonal pattern in frequency of appearance and number of stations with aggregations was similar in every year; they increased in June–July, peaked in August–September, and were mostly absent in December (Fig. 4.9.3).

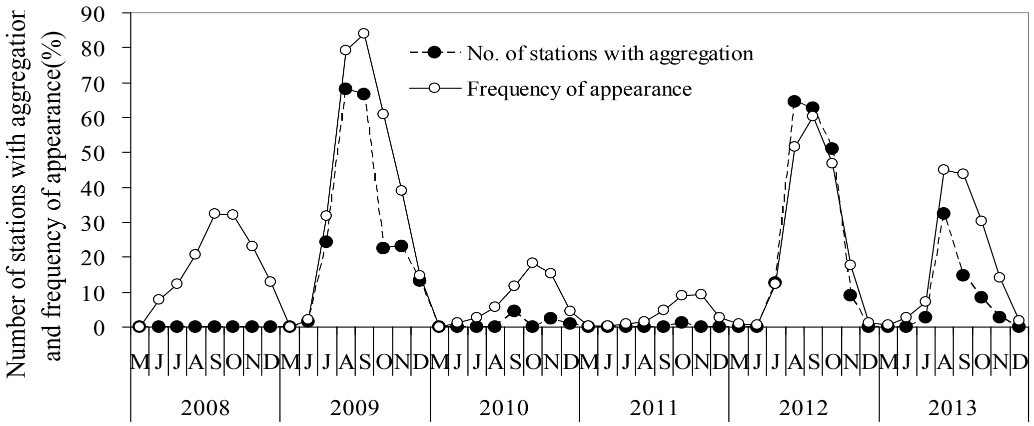


Fig. 4.9.3 Annual variations in frequency of appearance and number of stations with aggregations of *Nemopilema nomurai* from 2008 to 2013, based on the KoJEM surveys.

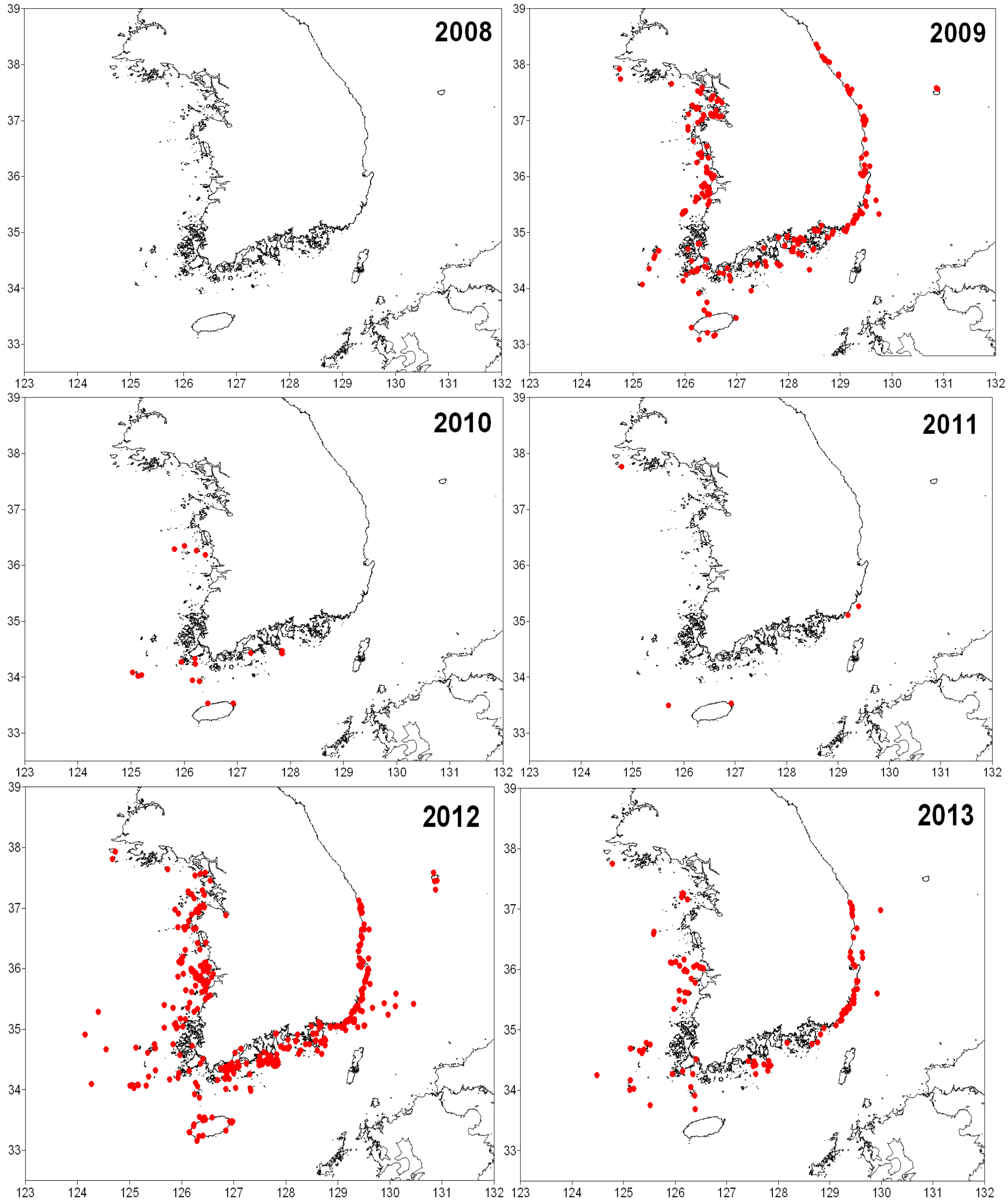


Fig. 4.9.4 Annual variations in station locations where *Nemopilema nomurai* were collected and their geographical distribution from 2008 to 2013, based on the KoJEM surveys.

Variability in appearance in offshore waters

The annual change in the average density of *N. nomurai* in August in the East China Sea and Yellow Sea, derived from KSO surveys, is shown in Fig. 4.9.5, together with the number of stations with aggregated *N. nomurai* in August derived from KoJEM surveys. They showed a similar trend of annual variation except during 2012 and 2013, when *N. nomurai* tended to be distributed in more offshore waters.

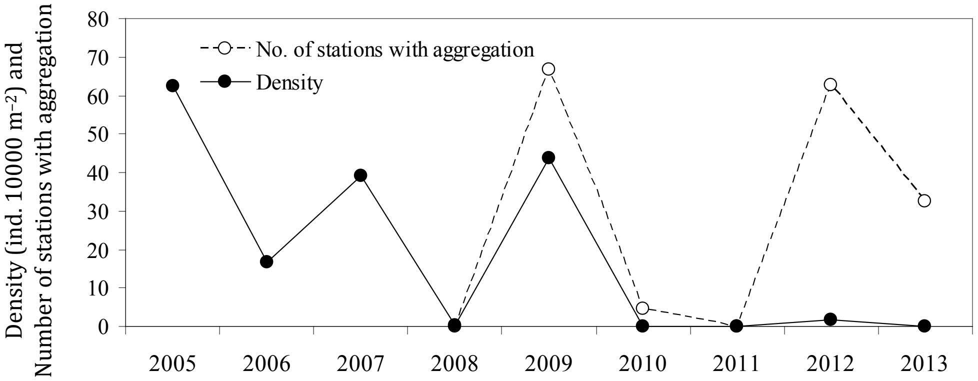


Fig. 4.9.5 Annual variations in average density of *Nemopilema nomurai* in the Yellow Sea and East China Sea, based on the KSO surveys, and the number of stations with aggregations in August in the coastal waters, based on the KoJEM surveys.

Migration in Korean waters

The distribution of *N. nomurai* in the East China Sea was determined by aerial surveys from June to August, 2013, and the monthly distribution of aggregations based on KoJEM data are depicted in Fig. 4.9.6. Large aggregations of *N. nomurai* were found in the northern East China Sea (31.5°–32.5°N, 125°E) on June 27–30 (Fig. 4.9.6a). The aggregations disappeared there but they appeared in Heuksando on July 17. At the same time, several small patches were observed in the area between the previous aggregations and the newly formed ones. After that, smaller aggregations were found along the southwestern coast of the Korean Peninsula from July 29 to August 16. Monthly distributions of aggregated *N. nomurai* also showed a similar pattern (Fig. 4.9.6b,c,d,e). Aggregations of *N. nomurai* were first observed around Heuksando in July (Fig. 4.9.6b) and were dispersed to all coastal waters including the east coast by August–September (Fig. 4.9.6c,d). In October, the aggregations disappeared from the east coast, but remained distributed along the west and south coasts (Fig. 4.9.6e).

The trajectory of *N. nomurai* from the East China Sea and the Yellow Sea was reproduced using the Jellyfish Tracking Model (model resolution: 0.1°) based on ROMS (Regional Ocean Modeling System) and LTRANS (Larval TRANSport Lagrangian model) (Fig. 4.9.7). The initial positions of *N. nomurai* were assumed to be in four locations (Fig. 4.9.7a): 1) the East China Sea where aggregations of *N. nomurai* were found at the end of May, 2013 (Yoon *et al*., 2014), 2) around the Changjiang River estuary, the most likely seeding location, 3) the central Yellow Sea, and 4) southern Yellow Sea.

The Jellyfish Tracking Model was operated from May 24 to August 24. The *N. nomurai* that originated in the East China Sea (off the Changjiang River estuary) were transported northwestward to Jeju Island in late June (Fig. 4.9.7b), and further transported northward to the southwest coast of the Korean Peninsula (Fig. 4.9.7c) where they were dispersed widely along the Korean west and south coast in July. In August, some of the medusae along the south coast were advected to the east coast (Fig. 4.9.7d). However, those *N. nomurai* that originated in the Yellow Sea did not approach Korean coastal waters.

The results of both monitoring surveys and physical modeling suggest that *N. nomurai* produced in the East China Sea, near the Changjiang River estuary, are primarily transported to Korean southwest coastal waters in June–July, and subsequently spread widely along Korean coastal waters, as shown schematically in Fig. 4.9.8.

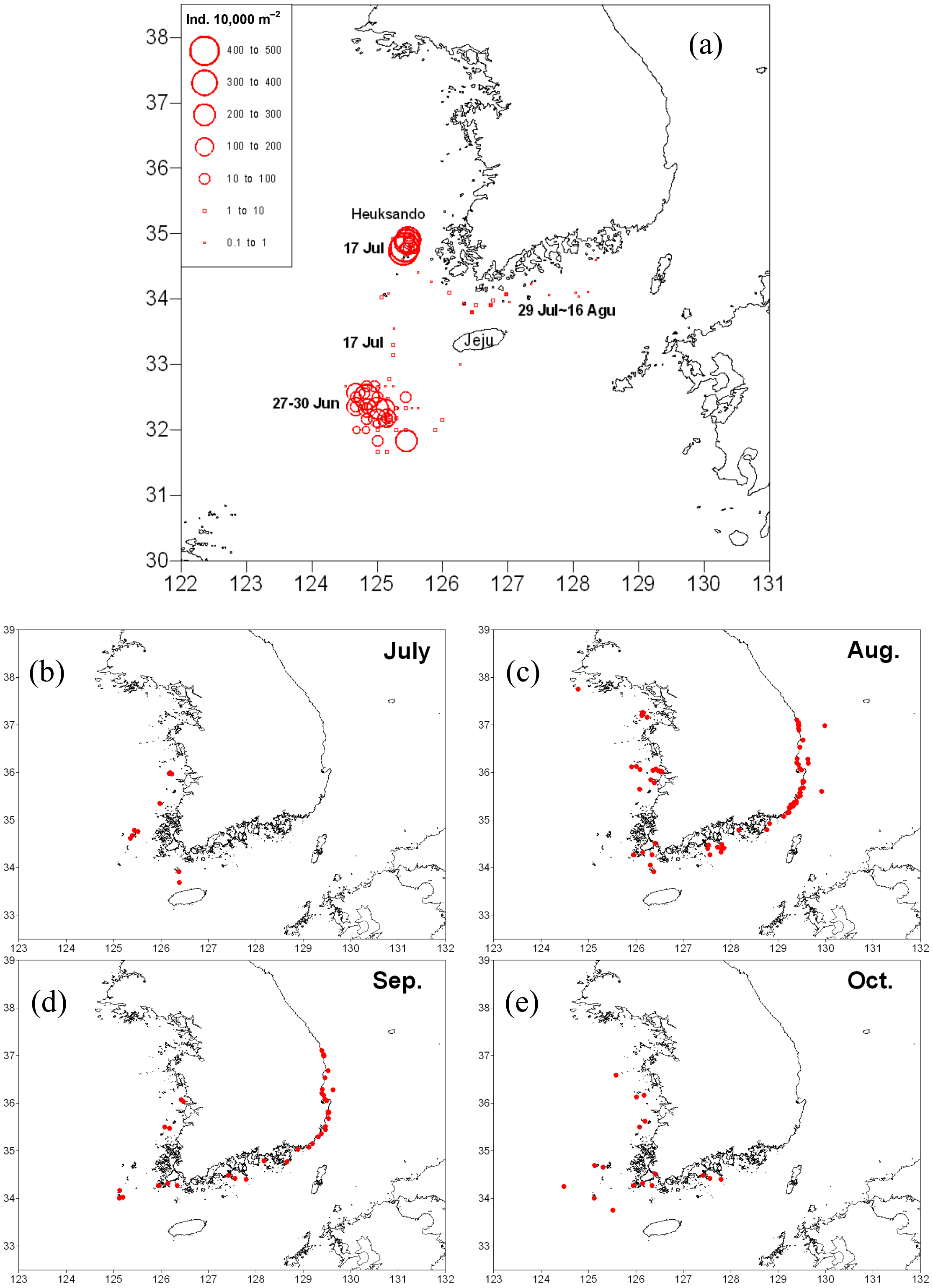


Fig. 4.9.6 Geographical distribution of *Nemopilema nomurai* in the East China Sea based on aerial surveys from June to August, 2013 (a), and monthly distribution of their aggregations from July to October, 2013 (b, c, d, e) based on KoJEM surveys.

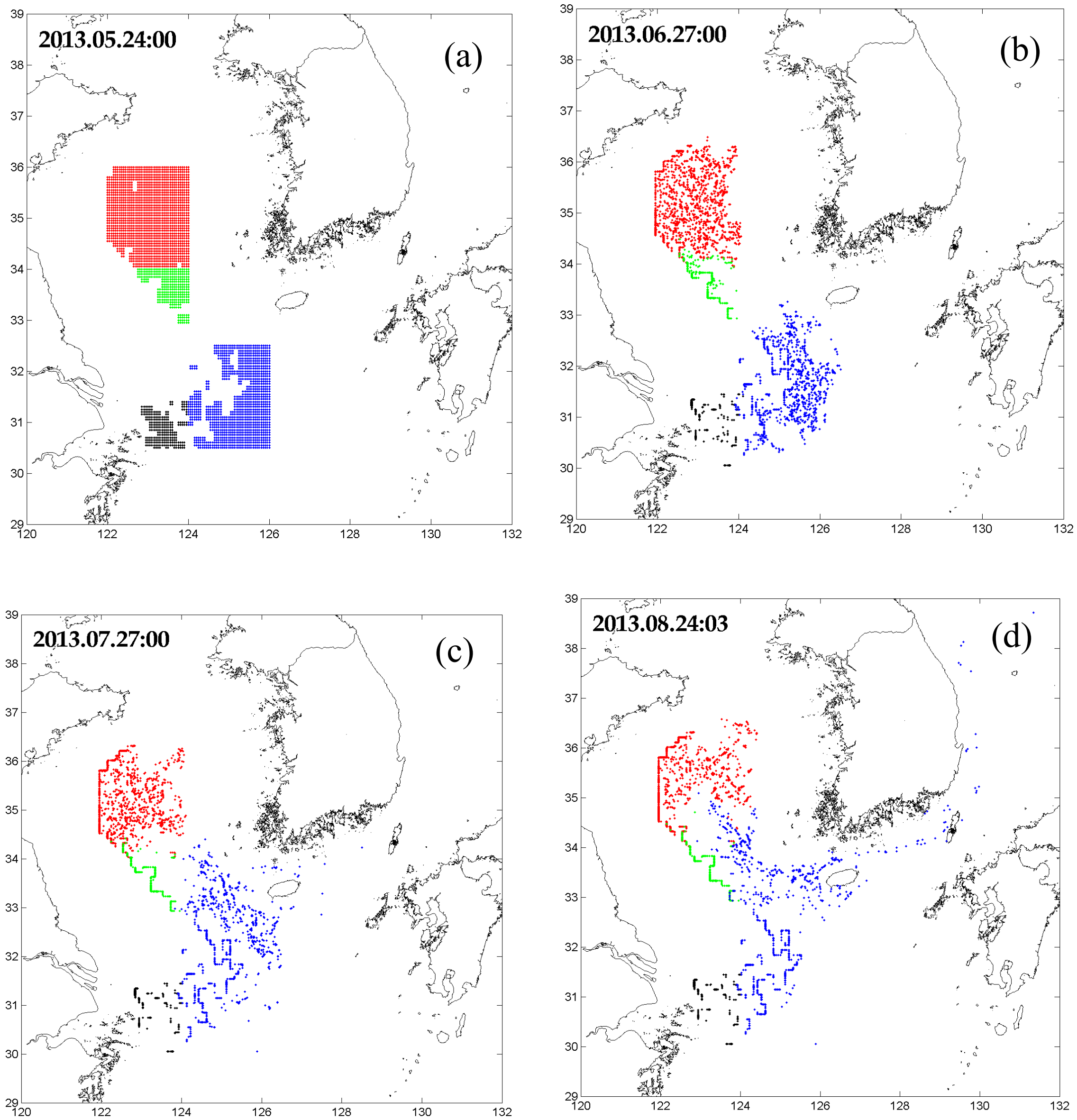


Fig. 4.9.7 Migration trajectory of *Nemopilema nomurai* using the Jellyfish Tracking Model based on ROMS (Regional Ocean Modeling System) and LTRANS (Larval TRANSport Lagrangian model). Aggregations of *N. nomurai* are denoted by red dots in the central Yellow Sea, green dots in East China Sea, blue dots in the East China Sea and black dots around the Changjang River estuary.

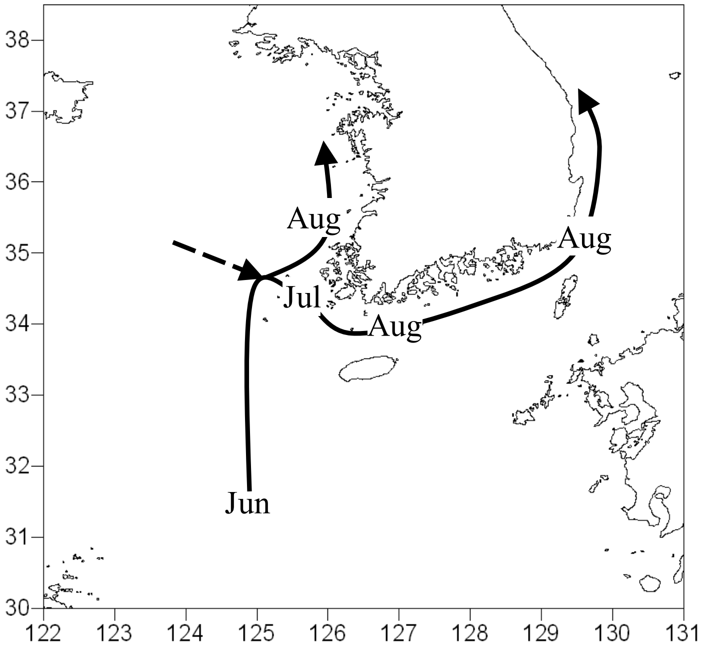


Fig. 4.9.8 Schematic representation of migration routes of *Nemopilema nomurai* from offshore in the East China Sea to Korean coastal waters. Solid lines indicate migration routes estimated from aerial data and the Jellyfish Tracking Model, and dotted line indicates possible migration route estimated from Japanese ferry survey data.

Aurelia sp. 1

The first noticeable bloom of *Aureli*a sp.1 occurred in 1996 when it caused a partial shutdown of the Uljin Nuclear Power Station located on east coast of Korea. Subsequent to that, some shutdowns and decreases of power production occurred until 2008 (Korean Nuclear Power Plant Operational Performance Information System, http://opis.kins.re.kr). At the same time, chronic blooming of this species has now become common in eutrophicated bays and inlets of the Korean Peninsula, such as Masan Bay, Sihwa Lake, and Saemangeum Lake (see Fig. 4.9.12 for locations). NIFS's polyp research project data indicate that these lakes and bays harbor enormous numbers of polyps and are likely to be a source of the medusae blooms.

Variability in appearance in coastal waters

Based on KoJEM surveys, the annual variation in frequency of appearance (number of stations with appearance/total number of stations) and number of stations where aggregated *Aurelia* sp. 1 occurred are depicted in Fig. 4.9.9. Seasonal trends of both parameters were very similar in every year ($r = 0.78$, $P < 0.05$); they increased in June–July, peaked in July–August and mostly disappeared by October. Although *Aurelia* sp. 1 has been abundant during summer in every year, the annual average number of stations with aggregations and scale of their distribution has decreased since 2009 except for a slight increase in 2012 (Fig. 4.9.10). This reduction appeared more remarkably along the west coast (Fig. 4.9.11), but the causes for the decrease are unknown. However, considering the recent increase in the number of stations with aggregations and their extended distribution in 2013, it is probable that *Aurelia* sp. 1 population size may change with some periodicity.

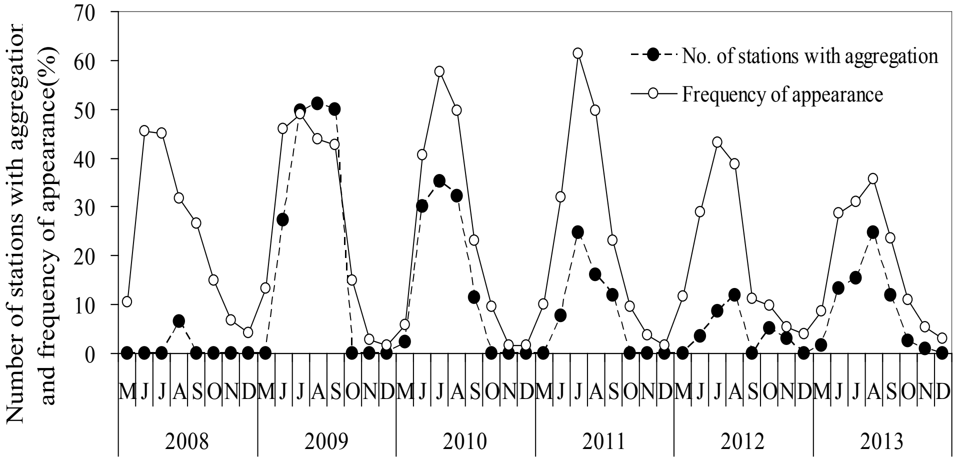


Fig. 4.9.9 Annual variation in frequency of appearance and number of stations of aggregated *Aurelia* sp. 1 from 2008 to 2013, based on KoJEM surveys.

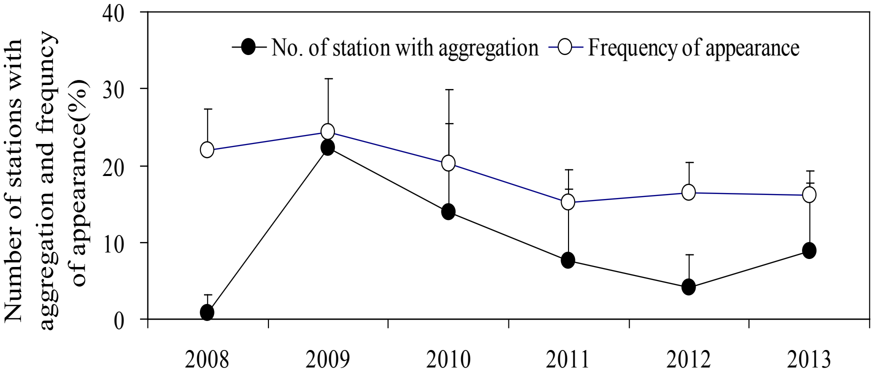


Fig. 4.9.10 Annual variation in average number of stations of aggregated *Aurelia* sp. 1 and frequency of appearance from 2008 to 2013, based on KoJEM surveys.

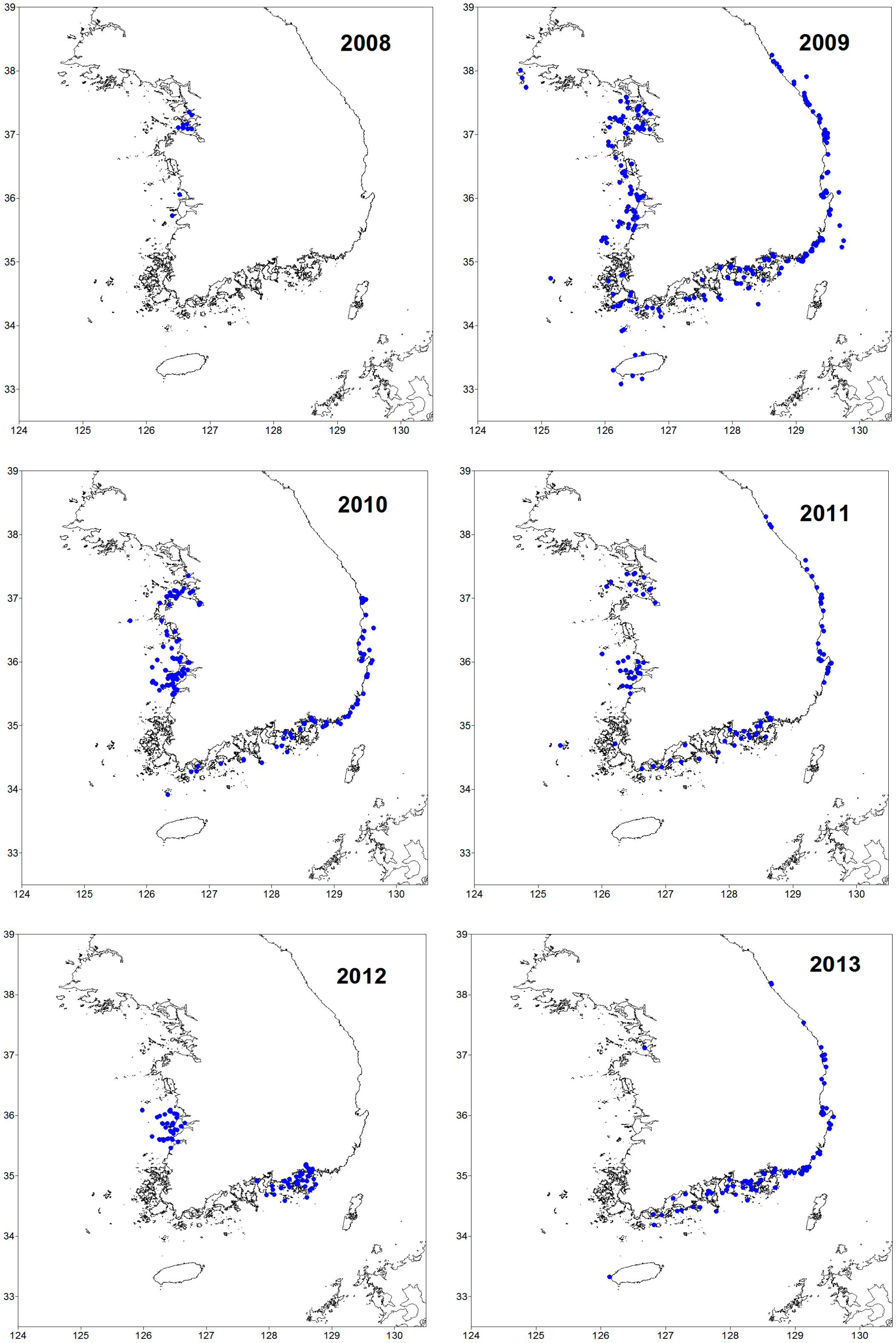


Fig. 4.9.11 Annual variations in station numbers of appearance of *Aurelia* sp. 1 and their geographical distribution from 2008 to 2013, based on KoJEM surveys.

Polyp hotspots

As outbreaks of *Aurelia* sp. 1 became more frequent, NIFS initiated research on the major habitat of *Aurelia* polyps to reveal the origin of the outbreaks in the coastal waters of Korea starting in 2009. The first polyp hotspot was found in Seamangeum Lake, which is enclosed by a 34 km long dike (Fig. 4.9.12). Most of polyps attached on ripraps along the dike, and the estimated total number of polyps along the dike was up to approximately 2.1 billion in 2009 and 2010 surveys. The second polyp hotspot was Sihwa Lake, a water body enclosed by an 11 km long dike. Most of the polyps in this area were attached to power transmission towers coated with plastic strung across the lake rather than on the riprap associated with the dikes. The estimated gross number of polyps in Sihwa Lake was approximately 120 million in 2011. Frequent outbreaks of medusae reported near these lakes from 2008–2013 (see Fig. 4.9.11) might be attributed to massive polyp populations inside the lakes. The most recently found hotspot was Masan Bay, a semi-enclosed bay surrounded by an ~14 km concrete wall where approximately 600 million *Aurelia* polyps were estimated to be attached in 2012. These analyses suggest that all polyp hotspots are associated with enclosed or semi-enclosed water bodies largely surrounded by artificial substrates such as dikes, concrete walls and plastics substrates.

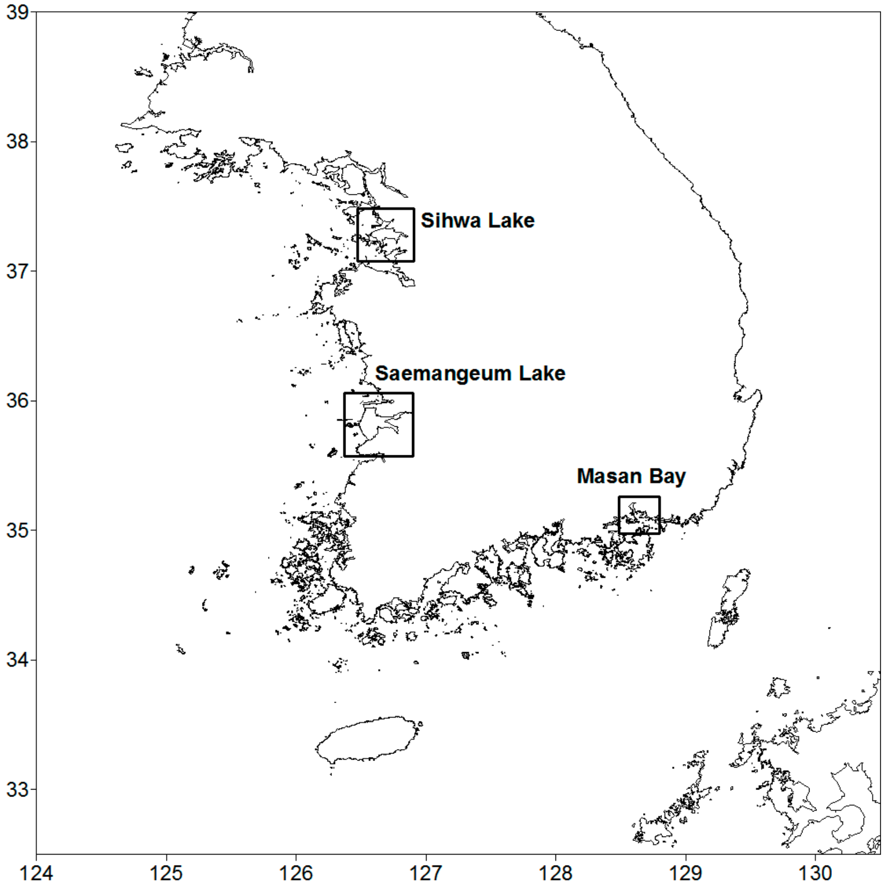


Fig. 4.9.12 Map of *Aurelia* sp. 1 polyp hotspots (frames) off the coast of Korea.

4.9.3 Stinging incidents

Jellyfish species causing stinging incidents in Korean coastal waters are primarily the scyphozoans *N. nomurai*, *Pelagia noctiluca* and *Chrysaora pacifica*, and the hydrozoan *Physalia physalis*, in addition to the cubozoan of the genus *Carybdea*. Among these, *N. nomurai* is presumed to be the most causative species in stinging incidents, with the others being minor components. The annual fluctuations in the number of stinging incidents in Haeundae Beach (southeast coast), the largest and most popular swimming beach in Korea, are significantly correlated to the average density of *N. nomurai* in Korean south coastal waters (*i.e.*, KSO data; see Fig. 4.9.2) from 2008 to 2011 (r = 0.75, p <0.05, Fig 4.9.13). However, in 2012 the number of stinging incidents noticeably increased in spite of the low density of *N. nomurai*.

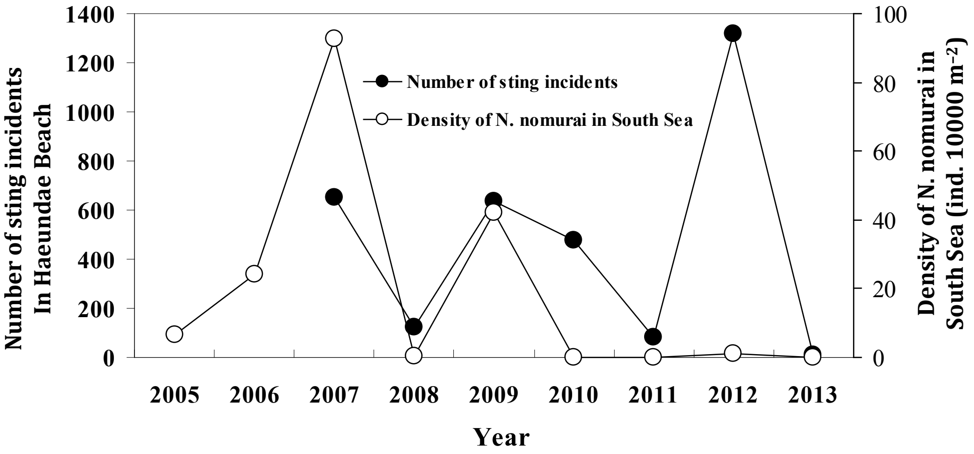


Fig. 4.9.13 Annual variation of stinging incidents by jellyfish in Haeundae Beach and the average density of *Nemopilema nomurai* in Korean south coastal waters, based on KSO data.

In order to understand this unusual stinging event in 2012, NIFS and the Korean Coastal Guard collected stinging incident data at 28 beaches from July 3 to August 11, 2013, and found that the incidences of stinging by *C. pacifica* and *Carybdea mora*, the latter of which has not been reported yet in Animal Systematics, Evolution and Diversity (Table 4.9.1), were much more serious than those by *N. nomurai* (Fig. 4.9.14). This suggests that the unusual case in 2012 was due mainly to stinging by *C. pacifica* and *C. mora*, which appear to have increased recently in Korean coastal waters.

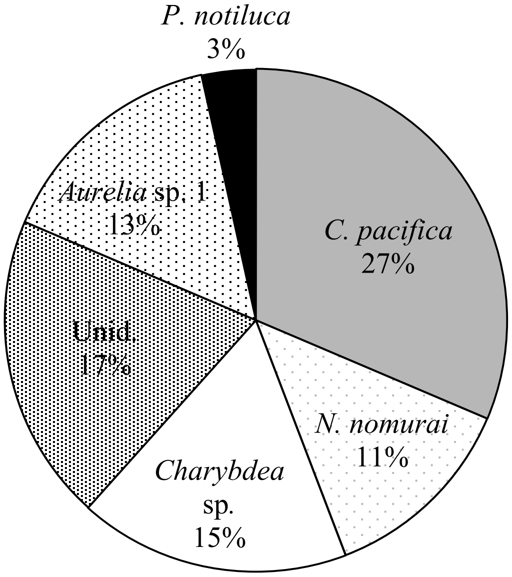


Fig. 4.9.14 Taxonomic composition of jellyfish inducing stinging incidents in 28 beaches along the Korean coast from July 3 to August 11 in 2003, based on a report from the Korean Coastal Guard.

4.9.4 Summary

In Korean waters, like in Chinese and Japanese waters, jellyfish blooms, particularly of *Aurelia* sp. 1 and *Nemopilema nomurai*, have become markedly problematic in recent decades, causing serious damage not only to fisheries but also to power plant operations and tourism. To tackle these problems, NIFS established the Jellyfish Information Center in 2005, which was re-formed in 2010 to the Jellyfish Monitoring and Countermeasure Center supported by the Ministry of Food, Agriculture, Forestry and Fisheries. National-level monitoring projects and related studies have demonstrated the year-to-year variations in jellyfish population size and the locations of hotspots of *Aurelia* sp. 1 polyps. Recurrent blooms of jellyfish, at least for *Aurelia* sp. 1, may be linked to increased anthropogenic habitats, preferred by polyps, along the Korean coast.

4.10 Chinese Coast

Song Sun and Fang Zhang

Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China

4.10.1 Introduction

Since the beginning of the 21st century, Chinese coastal waters have suffered from increased incidences of jellyfish blooms, which are considered to be among the most serious ecological disasters, together with harmful algae blooms (HABs), impacting the marine ecosystem, environmental safety, and the development of the maritime economy (Lucas *et al*., 2014; Sun *et al*., 2015a). To better understand the mechanisms for such a prominent increase in jellyfish blooms and to assess their ecological and economic impacts on the marine ecosystem, Chinese marine scientists participated in two large national-level research projects on jellyfish. The first was the Public Science and Technology Research Fund Project of Ocean, conducted by scientists of the National Bureau of Oceanography, China, from 2010 to 2014. The main objectives of this project were to develop monitoring techniques and prediction methods for jellyfish blooms. The other was a National Basic Research Program of China project entitled "The Key Processes, Mechanisms and Ecological Consequences of Jellyfish Blooms in Chinese Coastal Waters" which was conducted from 2011 to 2015 by the Ministry of Science and Technology, China. Although some detailed scientific contributions from these projects have been published elsewhere (*e.g.*, *Oceanologia et Limnologia Sinica* Vol. 43, 2012; *Nature* Vol. 514, 2014; *Hydrobiologia* Vol. 754, 2015), this section provides a brief overview of the major progress on jellyfish studies conducted in the Bohai Sea, Yellow Sea, and East China Sea, as well as Jiaozhou Bay.

4.10.2 Bohai Sea

The Bohai Sea is a semi-enclosed inland sea on the coast of North China with a total area of 77,284 km^2 and an average depth of 18 m (Fig. 4.10.1). It can be divided into four geographical areas: Liaodong Bay (area: 36,000 km^2), Bohai Bay (15,900 km^2), Laizhou Bay (6,967 km^2), and the Central Bohai Sea (18,417 km^2). More than 17 rivers enter the Bohai Sea, the largest one being the Huanghe River (also called the Yellow River), which empties into the Laizhou Bay. The water is deepest (~70 m) at the northern end of the Bohai Strait, a wide passage between the Liaodong and Shandong peninsulas extending into the Yellow Sea (Wei *et al*., 2004). The main physical processes affecting the ecosystem of the Bohai Sea include aeolian, tidal, and thermohaline circulations, water-column stratification during summer in deeper areas, vertical mixing in autumn and winter, and river discharges (Guan, 1994). The Bohai Sea is a productive area (primary production rate: ~100 g C m^{-2} yr^{-1}) (Guo, 1994) due to large nutrient loads from adjacent coastal lands with increased human populations and associated activities, in addition to the relatively slow replacement rate of the bay water. Hence, the ecosystem of the Bohai Sea has been degraded, as represented by extensive eutrophication, reduced biological diversity, more frequent red tides, benthic hypoxia, and a decrease in fish catches (Su and Tang, 2002).

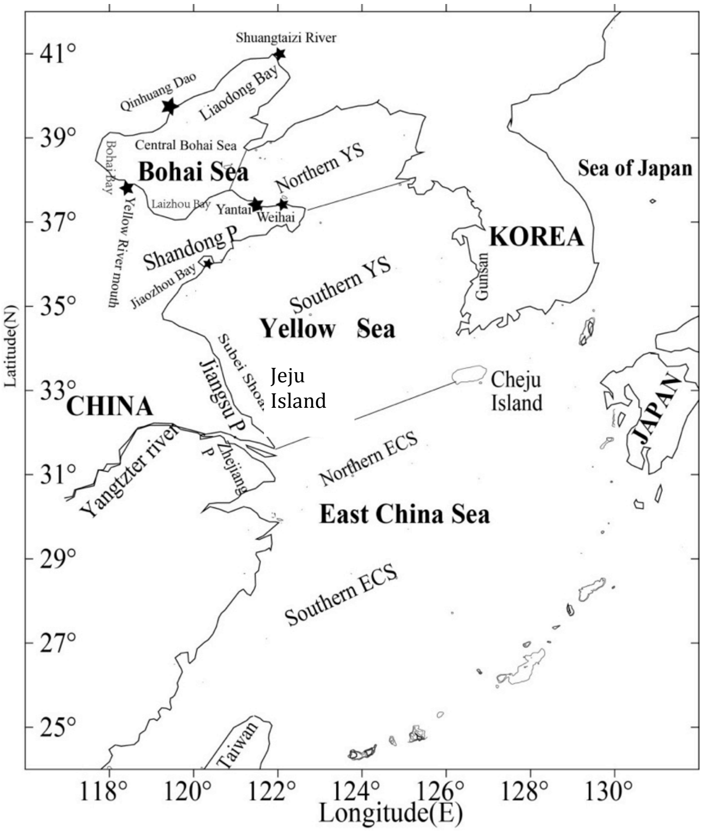


Fig. 4.10.1 Map of Chinese coastal waters showing the main bodies of water and subdivisions of the different regions (lines).

The Bohai Sea, a traditional fishing ground for the edible jellyfish *Rhopilema esculentum*, is also a habitat of other scyphozoan species such as *Aurelia aurita* s.1. (*i.e.*, *Aurelia* sp. 1, Dawson and Jacobs, 2001), *Cyanea nozakii*, and *Nemopilema nomurai*, which have all bloomed more extensively and frequently in the last few decades. *Aurelia* sp. 1 is distributed widely in coastal waters of the Pacific, *e.g.*, Australia, East Asia, California, and the Atlantic and Mediterranean coasts of France (Dawson and Martin, 2001). *Cyanea nozakii* occurs in the East Asian coastal waters mainly in summer (temperature range: 17–26°C, salinity range: 30–35) (Lu *et al.*, 2003; Ding and Cheng, 2007; Zhang *et al.*, 2012). Compared to *C. nozakii*, *N. nomurai* occurs over a much wider temperature rage (9–26°C, Gao *et al.*, 2002; Cheng *et al.*, 2005), and its geographical range extends to the East Asian Marginal Seas.

Long-term and seasonal variations in the occurrence of jellyfish

Although it is generally accepted that problematic blooms of large scyphozoan jellyfish have become more frequent and more extensive since the late 1990s in Chinese coastal seas, there are no systematic studies to document the long-term trend of jellyfish population abundance in the Bohai Sea. Available information is limited to several episodic bloom events in various areas of the bay.

For example, in July 2008, over 4,000 tons of *Aurelia* sp. 1 were cleared from the clogged intake screens of a power plant in Qinhuangdao, on the coast of the Bohai Sea, Hebei Province (Liu, 2008). In August 2008, 20–50 tons of *Aurelia* sp. 1 were also removed at a power plant in Weihai, on the coast of the

Yellow Sea, Shandong Province. According to Dong *et al*. (2013), although *Aurelia* sp. 1 generally blooms in the coastal waters of southern Liaodong Bay, its abundance was relatively low from 2004 to 2008, but increased in the northern part of the bay after 2009. In 2004, *C. nozakii* bloomed extensively in Liaodong Bay and caused serious damage in the production of the edible jellyfish, *R. esculentum*, the catch of which declined to 20% of the regular annual catch, resulting in a direct economic loss to approximately 70 million USD (Ge and He, 2004). However, after this big bloom in 2004, the abundance of *C. nozakii* appeared to decrease from 2005 to 2011 in the coastal waters of northern Liaodong Bay (Dong *et al*., 2013).

Massive blooms of *N. nomurai* have occurred in Liaodong Bay almost every year since the late 1990s. These blooms have serious impacts on the fishery resources of Liaodong Bay (Wang *et al*., 2013). Results of the investigations on the biomass of large jellyfish species (mainly *N. nomurai*) on the Hebei Province coast (including the Qinhuangdao area), which was supported by the Public Science and Technology Research Project, showed that biomass increased annually from 2008 to 2012, which had serious negative impacts on fisheries and coastal tourism (Zheng *et al*., 2014).

For *Aurelia* sp. 1, only fragmented information on population variation is available for this common jellyfish species in Liaodong Bay. Its seasonal occurrence appeared to be inconsistent between the northern and southern regions of the bay. In the northern region, juvenile medusae were not found until late May, but a massive number of medusae appeared relatively suddenly in late June, followed by a rapid decrease in July, whereas in the southern region, medusae occurred until September and then disappeared (Dong *et al*., 2013). According to a study conducted from 2005 to 2011 in Liaodong Bay (Dong *et al*., 2013), juvenile medusae of *C. nozakii* (bell diameter ~5 cm) usually occurred in early to mid-June, and grew to ~10 cm in bell diameter by the end of June and 15–20 cm by the end of July. They matured and spawned in August and September, and then suffered a die-off.

The innermost part of Liaodong Bay is thought to be one of the possible nursery areas of *N. nomurai* because their juvenile medusae were concentrated in the shallow estuary of the Shuangtaizi River (≤5 m deep) in June. A peak density of 667 ind. ha^{-1} was recorded in a survey using net hauls. The average density decreased markedly with the increase in body size to 5.1 ind. ha^{-1} in early July and to 1.8 ind. ha^{-1} in middle to late July. Their geographical distribution also shifted offshore, as few adult medusae were found in the area shallower than 5 m and more adults were found in waters 10–20 m deep (Wang *et al*., 2013), where *N. nomurai* medusae spawned from September to October when the water temperature decreased to 18–20°C, and then died off (Dong *et al*., 2013).

In conclusion, although substantial numbers of studies have been carried out on the occurrence and geographical distribution of the bloom-forming large jellyfish species in the last decade, available information is still insufficient to gain a complete picture of the temporal and spatial variations of each jellyfish species in the Bohai Sea. These properties found in each of four areas, Liaodong Bay, Bohai Bay, Laizhou Bay and the Central Bohai Sea, were not always consistent, which is partly due to different physico-chemical environmental features in these respective areas. Therefore, more systematic studies are needed for longer periods of time in order to understand the actual trends of jellyfish populations and the causes and consequences of jellyfish blooms in the Bohai Sea.

Long-term and seasonal variations in the occurrence of the edible jellyfish Rhopilema esculentum

Rhopilema esculentum has been commercially harvested for many decades in the Bohai Sea, and the fishery has been affected largely by human activities. The history of *R. esculentum* production can be divided into two periods: before, and after 1984, when stock enhancement via the release of cultured juveniles of *R. esculentum* commenced (Dong *et al*., 2009; Dong *et al*., 2014). From 1955, when the catch was first recorded, until 1975, the annual catch fluctuated between 0.01 and 0.06 million tons. Following 1975, there was a sharp decline due to overexploitation (Huang *et al*., 1985; Liu *et al*., 1992) and extremely low catches (≤0.03 million tons) continued until 1983 (Fig. 4.10.2). In order to meet the increasing demand for jellyfish, a pilot project of stock enhancement was conducted between 1984 and 2004 in Liaodong Bay (Chen *et al*., 1994; Liang *et al*., 2007). During the pilot trials, approximately 17.3 million juvenile medusae were released annually into the bay. In 2005, a large-scale enhancement project releasing 156 million juvenile medusae was conducted for the first time (Dong *et al*., 2009), and a similar scale of juvenile release was continued until 2010. Nevertheless, annual catches consistently declined to nearly half of the peak catch of 1998 (Fig. 4.10.2). The increase of *N. nomurai*, which is thought to be a competitor of *R. esculentum*, might explain the decrease in production of this edible jellyfish. On the other hand, concurrent changes in fishing effort and management practices (*e.g*., introduction of a fishing moratorium in 1995) might be a contributing factor to the stock enhancement program to increase jellyfish catch. It is generally accepted that the stock enhancement program has been successful in increasing the total catch of *R. esculentum* (Dong *et al*., 2009; Dong *et al*., 2014).

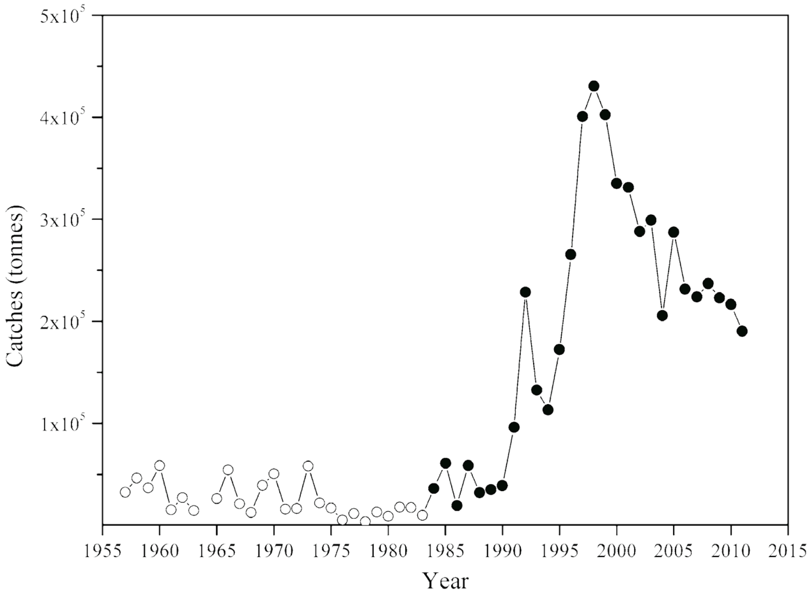


Fig. 4.10.2 Annual harvest of the edible jellyfish *Rhopilema esculentum* in Chinese waters, in tonnes wet weight. Open circles = harvest before stock enhancement; solid circles = harvest after stock enhancement (from Dong *et al*., 2014).

4.10.3 Yellow Sea and East China Sea

Jellyfish assemblages

The Yellow Sea (YS, area: 380,000 km^2, average depth: 44 m) and the East China Sea (ECS, area: 770,000 km^2, average depth: 72 m) are temperate marginal seas in the Northwest Pacific Ocean, both being semi-enclosed by the mainland of China in the west and Korean Peninsula and Korean and Japanese islands in the east. The two seas are connected topographically and oceanographically, but divided subjectively by a line from the Yangtze (Changjiang) River mouth to Jeju Island, Korea (Fig. 4.10.1). These two seas are not only very productive fishing grounds, but also major spawning, feeding and overwintering grounds for many economically important fish and crustacean species. The YS and ECS are the main fishery grounds in China and account for approximately 70% of the total fish catch in Chinese coastal seas. The YS and ECS have a broad continental shelf, and hydrographic conditions are affected by a huge run-off of terrigenous materials, mainly from the Changjiang River at the western boundary and by the Kuroshio Current flowing from the south, in addition to the East Asian monsoons (Tang and Su, 2000).

Out of a total of 45 large jellyfish species recorded in Chinese coastal seas (Hong and Lin, 2010), 10 species are commonly found in the YS and ECS: Scyphomedusae *Aurelia* sp. 1, *Cyanea nozakii*, *C. purpurea*, *Cyanea* sp., *Nemopilema nomurai*, *Parumbrosa polylobata,* and *Pelagia noctiluca* and Hydromedusae *Aequorea coerulescens*, *Aequorea* sp. 1, and *Aequorea* sp. 2, (Zhang *et al*., 2012). *Aequorea* spp., *Cyanea* spp., *N. nomurai*, and *P. polylobata* show a wider geographical distribution and greater biomass than the other species. Among these, *C. nozakii* and *N. nomurai* are the two major bloom-forming species over the YS and ECS, but the main bloom area of *C. nozakii* is confined to the ECS. Physical features are also important for the accumulation of jellyfish since high biomass values of *N. nomurai* and *C. nozakii* were often found along the temperature discontinuities formed around 30°–31°N. This further indicates the importance of the annual variation in the position of the convergence of the Yellow Sea Cold Bottom Water and the Kuroshio Current, which are forced by climate change (Zhang *et al*., 2012; Sun *et al*., 2015b).

Long-term variations of Cyanea nozakii and Nemopilema nomurai

Although *C. nozakii* and *N. nomurai* have increasingly formed blooms in summer and autumn in the southern YS and northern ECS since the end of the 1990s (Cheng *et al*., 2004, 2005; Yan *et al*., 2004; Ding and Cheng, 2005), these blooms have been variable, being very extensive in 2003 and much less extensive in 2004 and 2005 (Ding and Cheng, 2007; Li *et al*., 2007). In subsequent years, specifically *N. nomurai* produced massive blooms in 2006, 2007, 2009, and 2012 but did not bloom in 2008, 2010, 2011, 2013, and 2014 (Sun *et al*., 2015b). Figure 4.10.3 shows that *N. nomurai* blooms have varied from year to year in the last 10 years, and there is no clear increasing trend.

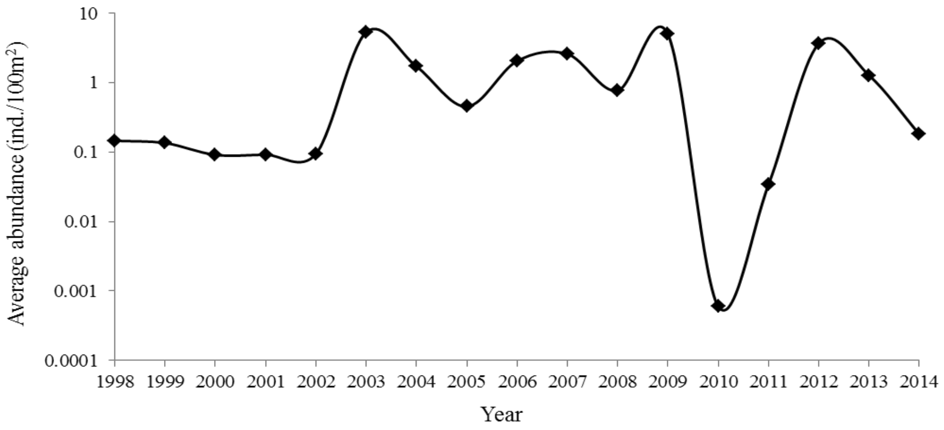


Fig. 4.10.3 Annual variation in abundance of *Nemopilema nomurai* in the southern Yellow Sea and northern East China Sea (summarized from Yan *et al*., 2004; Ding and Cheng, 2005; Li *et al*., 2007 and Sun *et al*., 2015a,b, and 2010 data from Uye's ferry results, unpubl.).

The general increase of *N. nomurai* blooms since the 1990s has had a significant impact on the fisheries of the YS and ECS (Cheng *et al*., 2004; Ge and He, 2004; Ding and Cheng, 2007). For example, in the autumn of 2003, *N. nomurai*, with an average biomass of 1,555 kg ha^{-1} and a maximum biomass of 15,000 kg ha^{-1}, depressed the catch per unit effort in the commercial fishery of small yellow croaker *Pseudosciaena polyactis* to 20% of the catch levels of the years without blooms (Ding and Cheng, 2005, 2007).

Seasonal occurrence and distribution of Cyanea nozakii and Nemopilema nomurai

An extensive field survey was carried out mainly as part of the China GLOBEC and China Jellyfish programs, which were conducted for almost 10 years, from 2006 to 2015. The results of the survey identified the seasonal occurrence and distribution patterns of *C. nozakii* and *N. nomurai* in the YS and the northern ECS. Although no ephyrae of *C. nozakii* were collected during the survey, a previous study (Zhou *et al*., 2004) showed that numerous young medusae of bell diameter ranging from 2 to 15 cm occurred annually from early March to May in the offshore waters of 30 to 31ºN, indicating that the major polyp habitat of *C. nozakii* in the ECS is probably located south of the Changjiang River. According to one survey (China GLOBEC Program), young *C. nozakii* medusae (bell diameter 4 to 50 cm) usually began to appear in early May in the coastal sea of the ECS, at least one month earlier than young *N. nomurai* medusae, which usually appeared in early June. The medusae of *C. nozakii* were mainly distributed in the southern area of the ECS (south of 29ºN) in May and were transported to the northern area with the coastal current from June to August. Therefore, the distribution pattern shifted more northerly (north of 29ºN) in June, July, and August. The overall abundance of *C. nozakii* reached an annual maximum in late May and early June, and then began to decrease thereafter (Zhang *et al*., 2012). The period of planktonic occurrence of this species is shorter than that of *N. nomurai*.

Results of another survey (Sun *et al*., 2015b) showed ephyrae of *N. nomurai* off the Changjiang River, indicating that this estuarine area appears to be one of the major polyp habitats of this species. Two locations were previously presumed polyp habitats based on the occurrence of ephyrae: one was the innermost part of Liaodong Bay (Wang *et al*., 2013; Zheng *et al*., 2014) and the other was the coastal waters offshore of Gunsan, Korea (Yoon *et al*., 2014). Based on the above information together with the data obtained in the surveys of Sun *et al*. (2015b)*,* the overall seasonal occurrence and geographical distribution of *N. nomurai* are schematically represented in Fig. 4.10.4.

Although ephyrae, metephyrae and juvenile medusae of *N. nomurai* appear in Chinese and Korean coastal areas in May and June, they first appear in the area offshore of the Changjiang River after which their appearance shifts northward to the area offshore of Gunsan, and finally to Liaodong Bay. The distribution pattern of *N. nomurai* expands progressively to about 31.5–36°N in the southern YS in June (no medusae were found in the northern YS), and then spreads northward to the whole YS as well as southward to 30°N in August. The population size decreases and the geographical range shrinks in October when the medusae gradually die off and disappear by winter. Their planktonic life span is thus less than one year (Sun *et al*., 2015b).

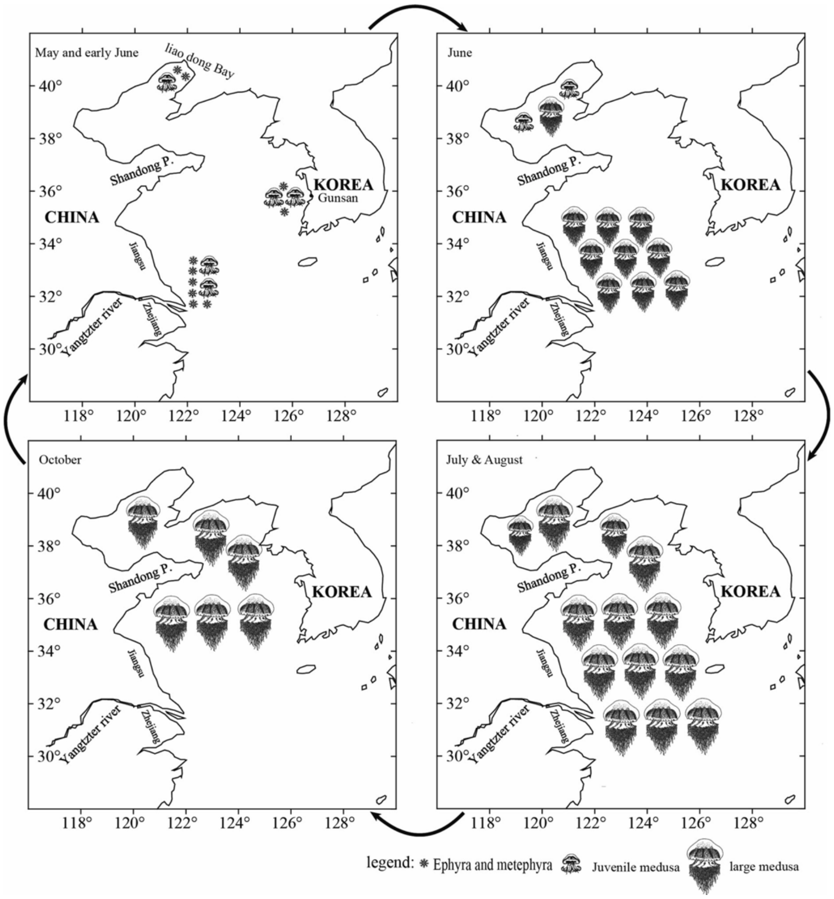


Fig. 4.10.4 Proposed annual variation in the distribution of *Nemopilema nomurai* in the East China Sea and Yellow Sea showing the increase and decrease of biomass from May to October (from Sun *et al*., 2015b).

Growth pattern of Nemopilema nomurai

The growth of *N. nomurai* was, in general, very fast. The overall seasonal growth pattern was similar among years, but the actual growth rate in each season varied by year. For instance, the growth rate was highest (ranging from 0.092 d^{-1} in 2009 to 0.185 d^{-1} in 2012) in early summer, decreasing (ranging from 0.020 d^{-1} in 2012 to 0.036 d^{-1} in 2013) from late June to late August, and thereafter became negative

(–0.013 d^{-1} in 2013). An inverse relationship between medusa body size and density was demonstrated for *N. nomurai* caught in late August; for example, the density and average bell diameters were 3,794 ind. km^{-2} and 63 cm, respectively, in 201, and the corresponding values were 689 ind. km^{-2} and 83 cm, respectively, in 2013 (Zhang, unpubl. data). This phenomenon might be attributed to the density effect of the medusan population — the higher the population density, the less food allowance per individual, but this is based on only two years of data so is somewhat preliminary.

4.10.4 Jiaozhou Bay

Jiaozhou Bay is a eutrophic semi-enclosed bay (area: 374 km^2, average depth: ~7 m) surrounded by Qingdao City, and connects to the western YS. In the past 40 years, the environmental condition and ecosystem of Jiaozhou Bay has changed, notably due to increased human activity and global climate change. The concentrations of nutrients, such as N and P, have changed substantially, resulting in shifts in phytoplankton species composition (Shen, 2006) as well as zooplankton assemblages (Sun *et al*., 2008). The average abundance of small jellyfish increased from 3.2 ind. m^{-3} during the period between 1991 and 2000 to 15.2 ind. m^{-3}, almost a fivefold increase, during the period between 2001 and 2009 (Sun *et al*., 2012). Although there are no quantitative data on the long-term variations of large jellyfish, there has been a significant increase in media reports concerning swimmers being stung by *C. nozakii* and *N. nomurai* in recent decades. In addition, on July 7 and 8, 2009, there occurred a severe clogging incident at the cooling water intakes of a coastal power plant in Qingdao by an aggregation of *Aurelia* sp. 1, and over 10 tons of medusae were removed from intake screens (Dong *et al*., 2010).

Seasonal life cycle of Aurelia sp. 1

In regard to the seasonal life cycle of *Aurelia* sp. 1 in Jiaozhou Bay, the following three studies were carried out: 1) from February to December 2009 by vertical net tows (Wan and Zhang, 2012), 2) from January to December 2011 also by vertical net tows (Wang and Sun, 2015), and 3) from August 1 to September 30, 2011, by visual observations at weekly intervals (Wang *et al*., 2012). Based on the results from these studies, the seasonal life cycle of *Aurelia* sp. 1 in Jiaozhou Bay can be summarized as shown in Fig. 4.10.4. Ephyrae occurred from May to June, when the water temperature ranged from 12 to 20°C. The distribution of ephyrae was mainly restricted to the coastal areas of the bay, and their abundance was higher in harbors than at offshore stations. The average water temperatures at the peak abundance of ephyrae and medusae were 20.6 and 25.2°C, respectively (Wan and Zhang, 2012). In July, the medusa population attained an annual peak and at the same time the average bell diameter was maximal; in August, they fell into senescence and their abundance and bell diameter decreased. The medusae died off by the end of September (Fig. 4.10.5).

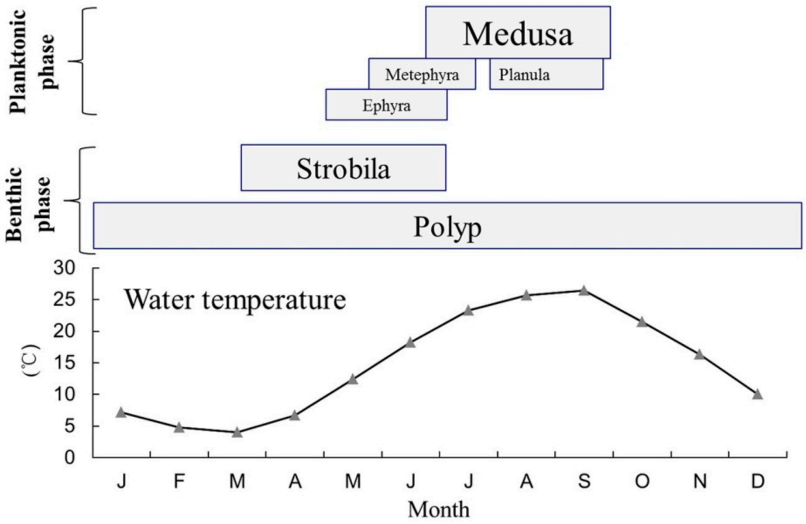


Fig. 4.10.5 Schematic representation of a typical seasonal life cycle of *Aurelia* sp. 1 in Jiaozhou Bay, China (from Wang and Sun, 2015).

Seasonal occurrences of Cyanea nozakii and Nemopilema nomurai

Since *C. nozakii* and *N. nomurai* were transported seasonally from the adjacent Yellow Sea to Jiaozhou Bay, their occurrence was examined by visual observations conducted twice per week from August 1 to September 30, 2011 (Wang *et al*., 2012). *Cyanae nozakii* occurred mainly in the inner part of the bay, whereas *N. nomurai* were mainly distributed near the bay mouth and in the central part of the bay. The abundance of *C. nozakii* and *N. nomurai* ranged from 0 to 150.2 ind. km^{-2} and 0 to 230.8 ind. km^{-2}, respectively (Wang *et al*., 2012).

Studies on the polyps of three scyphozoan jellyfish species

In order to evaluate the timing and environmental factors that induce strobilation and subsequent production of ephyrae of *C. nozakii* and *N. nomurai* in Chinese coastal waters, polyps of these species that were allowed to artificially settle on plates in the laboratory were placed in Jiaozhou Bay and monitored from December 2012 to August 2013 (Feng, unpubl. data). The strobilation of *N. nomurai* started from the middle of April and ceased by early June when the seawater temperature increased from 9 to 18 °C, whereas *C. nozakii* started from the middle of May and ceased by the middle of July when the temperature ranged from 15.6 to 21°C. Some *N. nomurai* polyps produced a second strobilation in early May. The cumulative percentage of the polyps which conducted the first strobilation was 72%, with 25.8% in the second strobilation. Ephyra production peaked in early May when the ambient temperature was 12°C, which was consistent with the temperatures observed in the laboratory experiment (Feng *et al*., 2015).

Benthic polyps in Jiazhou Bay were investigated by SCUBA diving from April 2013 to November 2014. Scyphozoan polyps found in the bay were only those of *Aurelia* sp. 1; those of *C. nozakii* and *N. nomurai* were never discovered. *Aurelia* sp. 1 polyps attached in an upside-down position not only to natural hard substrates such as oyster and mussel shells, but also extensively to the undersides of artificial substrates such as floating piers and concrete constructions. A laboratory experiment confirmed that planulae of *Aurelia* sp. 1 showed a preference for attaching to artificial substrates such as nylon fishing nets and polyvinyl chloride (PVC) plastics (Feng, unpubl.). These results indicate that the increase of marine construction and plastic debris provides new substrates for polyps, and may constitute vital drivers of jellyfish blooms in Jiaozhou Bay.

4.10.5 Summary

Intensive research programs on large scyphozoan jellyfish species have been carried out by Chinese scientists in the past decade. These studies consisted of acquiring some very basic information such as the life cycle and spatio-temporal distribution of medusae, to the identification of the causes for the recurrent blooms as well as assessment of the blooms on the marine ecosystem. The studies on the benthic polyp stage were greatly advanced by a combination of laboratory rearing experiments and *in situ* observations and experiments. Important progress in the Chinese jellyfish programs has been reported elsewhere (*e.g.*, in *Oceanologia et Limnologia Sinica* Vol. 43, 2012; *Nature* Vol. 514, 2014; *Hydrobiologia* Vol. 754, 2015) and should be consulted for more details. This section gives only an overview of the general information in three representative bloom-forming species, *i.e.*, *Aurelia* sp. 1, *C. nozakii*, and *N. nomurai* in the Yellow Sea and East China Sea. As current knowledge is still insufficient to understand the mechanisms and ecological consequence of the jellyfish blooms, studies should be continued in order to properly manage the Chinese coastal marine ecosystems.

5 Physio-Ecological Properties of Jellyfish

Mary N. Arai[1], Richard Brodeur[2], Jennifer Purcell[3] and Shin-ichi Uye[4]

[1] Pacific Biological Station, Nanaimo, British Columbia, Canada
[2] Northwest Fisheries Science Center, Hatfield Marine Science Center, National Marine Fisheries Service, NOAA, Newport, Oregon, USA
[3] Shanonn Point Marine Center, Western Washington University, Anacortes, Washington, USA
[4] Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Japan

5.1 Introduction

Prior to 1970, research on coelenterates was largely focused on taxonomy and behavior of the smaller hydrozoan medusa and ctenophores of the northern Pacific Ocean and Atlantic Ocean. In subsequent years, the feeding, respiration and growth of the larger hydrozoan siphonophores and the scyphozoan medusae were emphasized over a broader range of localities and environments. In 1997, three reviews described the contemporary knowledge of coelenterate food webs (Arai, 1997a,b; Purcell, 1997). Since then the knowledge of animal prey, respiration, and somatic growth has continued to grow for various locations but other topics, such as anaerobic metabolism and reproductive products, have still had little attention.

5.2 Metabolic estimates

Metabolism is the chemical processes that occur within a living organism in order to maintain life and can be defined as the sum of all processes through which protoplasm is formed from food (*i.e.*, anabolism) and broken down into waste matter (*i.e*, catabolism), with release of energy. Energy gained through these processes is stored exclusively in the form of adenosine triphosphate (ATP) and is used for various activities (locomotion, production of new tissue, ion pumps*, etc.*) of living organisms. ATP is generated from the tricarboxylic-acid (TCA) cycle, for which oxygen is required to drive the organism. Therefore, metabolic rates can often be determined as oxygen consumption rates or respiration rates (Ikeda *et al.*, 2000). It is of physio-ecological interest to measure the metabolic rates of jellyfish, whose gelatinous bodies consist of extraordinarily high water content (*i.e.*, ~96% of body wet weight, Lucas *et al.*, 2011), and compare the rates with those of solid bodied animals such as crustaceans and fish, which contain water of roughly 80% of wet weight (Omori, 1969; http://www.fao.org/wairdocs/tan/x5916e/x5916e01.htm), in order to characterize the physio-ecological properties of jellyfish as an important component of the zooplankton community in the marine pelagic realm.

As one of the main objectives of research on jellyfish is to determine their functional roles in the marine food web, it is basically necessary to estimate their feeding impact on prey organisms. However, their fragile body structure and possession of long tentacles and/or oral arms often precludes measuring their feeding rates. An ecological merit to estimate the metabolic rates of jellyfish is to estimate their minimum food requirement to balance the metabolism. If data on numerical abundance, biomass and net growth rates of jellyfish are available in addition to the minimum food requirement, one can estimate the amount of food required by the jellyfish population to sustain the observed *in situ* growth rates, and further, the predation pressure to prey populations.

5.2.1 Scaling of respiration rates in relation to body mass

In the PICES region, respiration rates have been measured for 5 scyphozoan species: *Aurelia aurita* s.l. (Kinoshita *et al*., 1997; Uye and Shimauchi, 2005; Ishii and Tanaka, 2006; Han *et al*., 2012), *A. labiata* (Larson, 1987), *Cyanea capillata* (Larson, 1987; Rutherford and Thuesen, 2005), *Phacellophora camtschatica* (Rutherford and Thuesen, 2005) and *Nemopilema nomurai* (Kawahara and Uye, unpubl..; Purcell *et al*., 2010). As for method, medusae collected from the field or raised in the laboratory were individually incubated in airtight containers of various volumes filled with filtered seawater of near-saturated level of dissolved oxygen concentration (DO), and the DO was measured by Winkler titration or with a DO sensor before and after the incubation. At each temperature, a relationship between respiration rates (RR) and body weights, in terms of wet weight (WW) or dry weight (DW), was expressed by equations shown in Table 5.2.1. When the measurements were conducted at multiple temperatures, the effect of temperature (T) was also incorporated into the equations by using, for example, the Q_{10} temperature coefficient.

Purcell *et al*. (2010) compiled previously published data on respiration rates of 14 scyphozoan medusa species, including the above-mentioned species from the PICES region, of three suborders of Semeaostomeae (6 species: *A. aurita* s.l., *A. labiata*, *Chrysaora quinquecirrha*, *C. capillata*, *Pelagia noctiluca* and *P. camtschatica*), Rhizostomeae (6 species: *Cassiopea xamachana*, *Catostylus mosaicus*, *Mastigias* sp., *N. nomurai*, *Rhizostoma pulmo* and *Stomolophus meleagris*) and Coronatae (2 species: *Linuche unguiculata* and *Periphylla periphylla*), and analyzed the relationship to individual body carbon weight, which ranged from approximately 2×10^{-6} g for an ephyra stage of *A. aurita* s.l. to approximately 47 g for an immature *N. nomurai* medusa, and experimental temperature, which ranged from 6 to 30°C. Multiple regressions showed that log-transformed respiration rates were not affected significantly by temperature, which was then excluded from the analysis, but by medusa body carbon weight. Hence, the respiration rates could be expressed by the following allometric equation:

$$RR = 83.37 \times CW^{0.940} \ (R^2 = 0.943),$$

where RR (ml O_2 d^{-1}) is respiration rate and CW (g) is carbon weight (Fig. 5.2.1). The slope (*i.e.*, 0.940) was close to 1.0, indicating that the carbon weight specific respiration rate is nearly constant irrespective of medusa size.

Table 5.2.1 Respiration rates (RR) of scyphomedusae from the PICES regions as functions of body wet weight (WW) or dry weight (DW) and temperature (T).

Species	Temperature (^{o}C)	Wet weight range (g)	Equation	Reference
Aurelia aurita s.l.	10	0.004–0.41	$\ln RR\ (\mu l\ O_2\ h^{-1}) = -1.287 + 0.58 \times \ln mg\ DW$	Kinoshita *et al*., 1997
	10	0.41–22.2	$\ln RR\ (\mu l\ O_2\ h^{-1}) = -1.990 + 0.89 \times \ln mg\ DW$	
	15	0.002–0.34	$\ln RR\ (\mu l\ O_2\ h^{-1}) = -0.905 + 0.63 \times \ln mg\ DW$	
	15	0.34–58.3	$\ln RR\ (\mu l\ O_2\ h^{-1}) = -1.634 + 0.93 \times \ln mg\ DW$	
	20	11.8–888.2	$RR\ (ml\ O_2\ d^{-1}) = 0.0401 \times gWW^{1.059}$	Uye and Shimauchi, 2005
	28	76.5–1338.2	$RR\ (ml\ O_2\ d^{-1}) = 1.396 \times gWW^{0.777}$	
	Combined		$RR\ (ml\ O_2\ d^{-1}) = 0.0765 \times 2.8^{(T\text{-}20)/10} \times g\ WW^{1.038}$	
	15	137–431	$RR\ (ml\ O_2\ h^{-1}) = 0.04 \times g\ DW^{1.399}$	Ishii and Tanaka, 2006
	20	78–397	$RR\ (ml\ O_2\ h^{-1}) = 0.167 \times g\ DW^{1.002}$	
	24	65–483	$RR\ (ml\ O_2\ h^{-1}) = 0.429 \times g\ DW^{0.877}$	
	Combined		$RR\ (ml\ O_2\ h^{-1}) = 10^{\ (0.11T\text{-}3.1)} \times g\ DW^{1.093}$	
	20	8– ~160	$RR\ (ml\ O_2\ d^{-1}) = 0.210 \times gWW^{0.849}$	Han *et al*., 2012
	28	~30–220	$RR\ (ml\ O_2\ d^{-1}) = 0.466 \times gWW^{0.846}$	
	Combined		$RR\ (ml\ O_2\ d^{-1}) = 0.13 \times gWW^{0.93}$	
Aurelia labiata	10	0.3–168.4	$\text{Log}\ RR\ (\mu l\ O_2\ h^{-1}) = 0.2 \times \log mg\ DW^{0.92}$	Larson, 1987
	15	0.3–89.5	$\text{Log}\ RR\ (\mu l\ O_2\ h^{-1}) = 0.39 \times \log mg\ DW^{0.91}$	
Cyanea capillata	10	0.5–385.7	$\text{Log}\ RR\ (\mu l\ O_2\ h^{-1}) = 0.47 \times \log mg\ DW^{1.0}$	Larson, 1987
	15	0.3–18.1	$\text{Log}\ RR\ (\mu l\ O_2\ h^{-1}) = 0.72 \times \log mg\ DW^{1.04}$	
	10	0.26–1.17	$RR\ (\mu mol\ O_2\ g\ WW^{-1}\ h^{-1}) = 0.78$	Rutherford and Thuesen, 2005
Phacellophora camtschatica	10	0.54–1.85	$RR\ (\mu mol\ O_2\ g\ WW^{-1}\ h^{-1}) = 0.13$	Rutherford and Thuesen, 2005
Nemopilema nomurai	24	1.2–9.6	$RR\ (ml\ O_2\ d^{-1}) = 0.781 \times g\ DW^{0.675}$	Kawahara and Uye, unpubl.; Purcell *et al*., 2010
	24	800–7800	$RR\ (ml\ O_2\ d^{-1}) = 1.491 \times g\ DW^{0.880}$	
	Combined		$RR\ (ml\ O_2\ d^{-1}) = 0.549 \times g\ DW^{1.0}$	

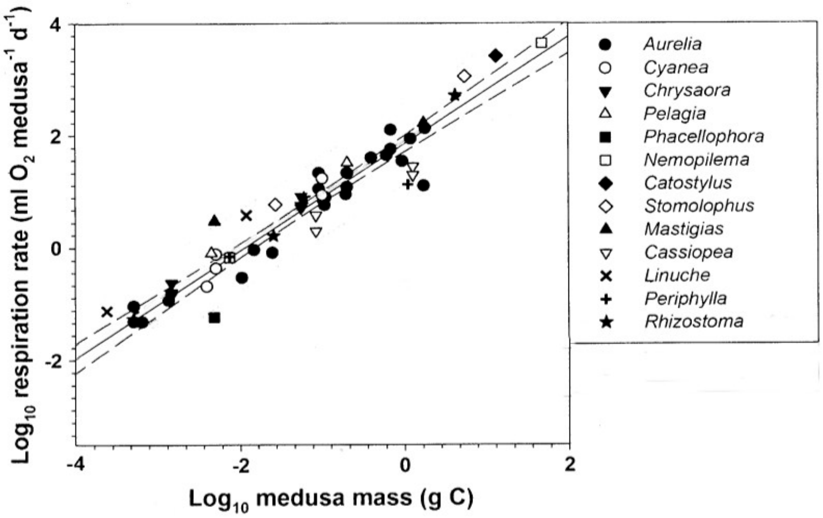


Fig. 5.2.1 Log-log relationship between respiration rate (RR, ml O_2 d^{-1}) and body carbon weight (CW, g) for 13 species of scyphozoan jellyfish species: $RR = 83.37 \times CW^{0.940}$ ($R^2 = 0.943$) (from Purcell *et al.*, 2010).

This allometric equation is a powerful tool to estimate the minimum food requirements of any scyphomedusan species from only body carbon weight. Meanwhile, wet weights are a common measure to determine medusa biomass, particularly in the field surveys, and the wet weight values should be converted to carbon weights for assignment into the above-mentioned allometric equation. For the conversion, Lucas *et al.* (2011) collated available data and calculated the mean conversion factors from wet weight to dry weight and from dry weight to carbon weight, which were 4.17 ± 1.39% (n = 41) and 10.03 ± 5.33% (n = 33), respectively. Because there are considerably wide variations among species and geographical locations, particularly related to habitat salinity differences (Hirst and Lucas, 1998), it is highly recommended to determine the carbon content or the conversion factors for target jellyfish species.

5.2.2 Minimum food requirement

Carbon weight specific minimum food requirement can be estimated as:

$$SMFR = (k \times RR \times RQ)/(A \times CW),$$

where $SMFR$ is specific minimum food requirement (d^{-1}), k is constant (5.36×10^{-4} g C ml^{-1} O_2), RR is respiration rate (ml O_2 d^{-1}), RQ is respiratory quotient (assuming 0.85 due to protein-dominated metabolism, according to Schneider (1989a,b)), A is assimilation efficiency (assuming 0.8, according to Schneider (1989a)) and CW is carbon weight of a medusa (g). $SMFR$ is calculated to be 0.055, 0.047 and 0.041 d^{-1} for a medusa of 0.1, 1.0 and 10 g carbon weight (~25, 250 and 2500 g wet weight), respectively, indicating that scyphozoan medusae require a minimum food amount of approximately 5% of their own carbon biomass per day. If medusae are able to ingest more than this amount, excess carbon can be used for their net growth for somata and/or reproduction.

5.3 Predation by jellyfish and their diets

Gelatinous zooplankton occupy a very wide range of roles in pelagic (and benthic) food webs. Robison (2004) noted that there tend to be two types of gelatinous predators, those that feed largely on crustaceans (typically copepods and euphausiids, of all life history stages) and those that feed largely on other gelatinous animals (often with a great deal of specialization). Siphonophores are often grouped among the former, with smaller taxa typically engaging in active feeding strategies and larger species often feeding using passive methods.

There have been a limited number of gelatinous zooplankton diet studies from the California Current. Suchman *et al*. (2008) analyzed *Chrysaora fuscescens, Phacellophora camtschtica,* and *Aurelia labiata* diets collected in August 2002 in relation to available plankton. They found that euphausiid eggs, cladocerans, and other gelatinous taxa were particularly important in the diets and that these medusae had the potential to remove 10–12% of the standing stocks of these prey per day. More recent work on *C. fuscescens* conducted in June, July and September of 2014 shows that certain prey types are more vulnerable to predation by jellyfish (Zeman, 2015). Gut content analysis of the medusae showed positive prey selection for vulnerable, slow-moving taxa, *e.g*., fish and invertebrate eggs, appendicularians. Predation on ichthyoplankton was particularly high in June when medusae are growing rapidly and fish eggs are abundant in the plankton. Copepods, though abundant in the plankton, were negatively selected relative to their availability in the plankton (Zeman, 2015).

There also is relatively little known about the diets of the dominant jellyfish species in the Bering Sea. Hamner (1983) reported gut contents for the predominant eastern Bering Sea Hydromedusae and Scyphomedusae. *Chrysaora melanaster* fed primarily on pteropods and on euphausiids, medusae and crustacean zooplankton. Larger (7–50 cm bell diameter) *C. melanaster* were also observed consuming juvenile walleye pollock (*Theragra chalcogramma*). *Cyanea* sp. consumed the hydromedusans *Euphysa flammea* and *Sarsia princeps* and scyphozoans *C. melanaster* and *Aequorea* sp. Pteropods, crustaceans and larval fish were also found in *Cyanea* sp. guts; however, it was not possible to determine if *Cyanea* sp. were feeding directly on these prey or if these items were the prey of the medusae consumed by *Cyanea* sp. The leptomedusan *Staurostoma mertensii* fed nearly exclusively on *Pseudocalanus* copepods, whereas *Aequorea* sp. fed upon mesozooplankton (*i.e*., copepodites, zoeae and juvenile pteropods). Laboratory and field observations indicate that the anthomedusans *Catablema* sp. and *Stomotoca atra* also feed on other medusa. Brodeur *et al*. (2002) found walleye pollock juveniles in about 20% of the *C. melanaster* stomachs examined during two different years, but no other fish species were identified. They estimated that this species was consuming 2.8% of the pollock on a daily basis. They also estimated that *C. melanaster* consumed roughly 32% of the standing stock of zooplankton on the shelf during summer, and as such could be a substantial competitor with many pelagic species. These pollock consumption values were much higher than those (0.03% of pollock eggs and 0.003% of the larvae) calculated for the Sea of Okhotsk by Gorbatenko *et al*. (2009).

In the western Bering Sea, jellyfish collected from trawls in fall 2006 generally contained zooplankton (copepods, euphausiids, amphipods, pteropods, chaetognaths, ostracods, and larval decapods, Table 5.3.1). However, *C. melanaster* guts also contained lanternfish and unidentified fish in its diet unlike the other jellyfish species examined (Zavolokin *et al*., 2008). Clearly more information is needed on the feeding ecology and predation potential of jellyfish upon fish species, especially in the spring when fish eggs and larvae are present in the water column.

Table 5.3.1 Summary of dominant jellyfish diets (% by weight) in the western Bering Sea in September–October 2006. Summaries by major taxonomic groups are in bold.

Prey	***Aequorea* sp.**	***Aurelia* sp.**	***Chrysaora melanaster***	***Cyanea* sp.**	***Phacellophora camtschatica***
Copepoda	**59**	–	–	**10**	–
Pseudocalanus sp.	+	–	–	–	–
Pareuchaeta japonica	+	–	–	–	–
Neocalanus plumchrus	57	–	–	–	–
Neocalanus cristatus	–	–	–	10	–
Metridia pacifica	2	–	–	–	–
Euphausiacea	–	–	**3**	**2**	**85**
Euphausia pacifica	–	–	2	–	85
Thysanoessa longipes	–	–	1	2	–
Euphausia sp.	–	–	+	–	–
Amphipoda	**35**	–	**+**	**5**	–
Themisto pacifica (1–2 mm)	–	–	+	5	–
Themisto pacifica (2–3 mm)	35	–	–	–	–
Themisto pacifica (3–4 mm)	+	–	+	–	–
Chaetognatha	**3**	–	–	–	–
Sagitta elegans	3	–	–	–	–
Pteropoda	**1**	–	**+**	**5**	–
Limacina helicina	1	–	+	5	–
Ostracoda	–	–	**50**	**-**	–
Decapoda zoea	**2**	**100**	**13**	**78**	**15**
Cephalopoda paralarvae	–	–	**2**	–	–
Teleosts	–	–	**32**	–	–
Stenobrachius leucopsarus	–	–	32	–	–
Unidentified fish bones	–	–	+	–	–
SCI ‱	0.53	0.07	0.70	1.18	0.16
Mean bell diameter (cm)	20.2	16.3	38.2	26.6	36.5
Mean weight (g)	444	327	2515	946	2300
Number of stomachs	11	5	6	8	2

SCI (Stomach Content Index) = prey weight × 10,000/body weight, ‱, or parts per decimile).
Postive signs denote < 0.5%; dashes indicate zeros.

5.4 *Predation on jellyfish*

In addition to being preyed upon by other gelatinous predators, many species of jellyfish are predated on, at times substantially, by fish and higher trophic level predators. Although some large-scale surveys (Mianzan *et al*., 1996) or literature reviews (Kashkina, 1986; Purcell and Arai, 2001; Arai, 2005) have shown gelatinous taxa to be important to many different predators, documentation of fish feeding on jellyfish has been limited for most marine ecosystems. In a search of the extensive FishBase online database (http://www.fishbase.ca/), Pauly *et al*. (2009) found only 124 species known to consume jellyfish, of which 11 eat mostly gelatinous forms. As a result, jellyfish are often ignored or considered trophic "dead ends" in many ecosystem models (Pauly *et al*., 2009).

In the California Current, several species of rockfish (*Sebastes*), particularly widow, yellowtail, black and blue rockfish, are known predators of a wide range of gelatinous plankton, particularly thaliacians, but including a broad range of cnidarians, ctenophores and other gelatinous macrozooplankton (Steiner, 1979; Brodeur and Pearcy, 1984; Adams, 1987; Lee *et al*., 2002). Laidig *et al*. (1997) also noted that sablefish (*Anoplopoma fimbria*) caught in California waters preyed on both salps and gelatinous zooplankton, although neither constituted a substantial fraction of the total prey biomass.

Numerous studies have examined the diets of many of the dominant groundfish species in the Bering Sea. Mito *et al*. (1999) summarized diet information on 64,652 fish from 47 species collected on the eastern Bering Sea shelf from 1972 to 1975. The only species they found which consumed appreciable amounts of medusae was prowfish (*Zaproa silenus*, n = 56), which consumed only gelatinous material. Brodeur and Livingston (1988) examined the diets of 25 elasmobranch and fish predators (n = 2,242) from the eastern Bering Sea in 1985 and 1986 and found that four species (sablefish *Anoplopoma fimbria*, yellow Irish lord *Hemilepidotus jordani*, flathead sole *Hippoglossoides elassodon*, and Alaska plaice *Pleuronectes quadrituberculatus*) consumed jellyfish but the frequency of occurrence and weight percentage of jellyfish eaten were low, generally less than 1%. An assessment of the Alaska Fisheries Science Center RACE demersal fish diet database (1985–2011) found 20 species had consumed Scyphozoa (mainly Alaska plaice, sablefish, walleye pollock and yellowfin sole), 16 species had eaten Ctenophora (primarily sablefish, walleye pollock, and snailfishes), and only 3 species had consumed salps (data provided by Troy Buckley, AFSC, Seattle). Stomachs that were analyzed fresh at sea often contained a higher proportion of gelatinous prey than those that were preserved and analyzed in the lab, suggesting rapid breakdown of gelatinous material and hence underestimates of the contribution of these prey to predators (Brodeur *et al*., 2014).

Pelagic fish predators on gelatinous taxa have also been reported for the Bering Sea. Many common myctophids, and especially bathylagid midwater fishes, are known to consume medusae and ctenophores, although gelatinous prey are secondary to crustacean prey (Gorbatenko and Il'inskii, 1992; Balanov, 1994; Balanov *et al*., 1995). In addition, juvenile and adult salmon are known to consume gelatinous prey, particularly chum salmon (Azuma, 1992; Sakai *et al*., 2012), and this may allow them to avoid competition with other salmon despite the low nutritive value of jellyfish (Davis *et al*., 1998).

However, as noted by Arai *et al*. (2003), the proportionately faster digestion rates of gelatinous zooplankton likely result in an underestimate of the relative role of these animals in food webs using traditional analysis. This is not a problem in considering what is among the most important roles of large jellyfish in food webs in this region, as the western leatherback sea turtle *Dermochelys coriacea*, which has the largest range of any living reptile by virtue of greater thermal tolerance than other sea turtle species, is widely recognized as being a specialist on large scyphozoans. A substantial fraction of the Pacific leatherback population may migrate into the California Current in any given year (although due to the distances associated with some migratory patterns, such patterns may reflect multi-year cycles or movement patterns) where they forage largely on aggregations of *Chrysaora* and *Aurelia*. Most of the foraging behavior observed in tagged turtles has been observed to take place off central California, although central Oregon waters are also important habitat (Benson *et al*., 2007, 2011). Individual turtles may eat 20 to 30% of their body weight per day, and up to 1000 tons per individual per lifetime, with the total Pacific-wide consumption by turtles estimated to be on the order of two million tons per year (Jones *et al*., 2012). Consequently, a better understanding of turtle habitat requirements and the factors that drive changes in jellyfish abundance and distribution may lead to improved management measures that minimize fishing-related mortality and help to protect these high profile endangered species.

Harrison (1984) determined that scyphozoan jellyfish are preyed upon by 11 species of birds in the Bering Sea: *Fulmarus glacialis, Puffinus griseus, Puffinus tenuirostris, Oceanodroma furcata, Larus hyperboreus, Rissa tridactyla, Rissa brevirostris, Uria aalge, Uria lomvia, Aethia psittacula,* and *Aethia cristatella*. Birds ingested *Chrysaora* and *Cyanea*, as well as other unidentified medusae. Hyperiid amphipods, which are parasitic on scyphomedusae (Towanda and Thuesen, 2006) also contributed to avian diets. Harrison (1984) found that birds feeding on jellyfish contained a greater diversity of prey than non-jellyfish-eating birds and suggested that gelatinous zooplankton are important in structuring the Bering Sea food web. More recently, Sato *et al*. (2015) found that the thick-billed murre *Uria lomvia* fed preferentially on juvenile walleye pollock that were associated with *C. melanaster* in the eastern Bering Sea, based on video observations.

5.5 Parasites and disease

In addition to reciprocal feeding by coelenterates and vertebrate predation, there are various other types of interactions and grades of importance in food webs, and resulting terminology can be confusing; the reader should consult authorities such as Rohde (1932).

Parasitism is understood to be the close association between two organisms, one of which the parasite, depends on the other, the host, deriving some benefit from it without necessarily damaging it. Parasites usually eat some portion of the host and are usually smaller than their host. The type of interaction may differ at different stages of the life cycle of the parasite or the host. In phoresis one organism uses another as a means of transport without establishing a close association. In commensalism one organism uses food supplied in the external or internal environment of a host without otherwise affecting the host. In mutualism two organisms live together in a non-compulsory association and each may derive benefit from the association. In contrast, in symbiosis the two organisms derive benefit that they cannot live without.

An example of a somewhat more complex terminology and relationship of three species was described by Towanda and Thuesen (2006). They observed the ectosymbiotic behavior of the crab *Cancer gracilis* with its scyphomedusan host *Phacellophora camschatica* and a parasitoid amphipod *Hyperia medusarum*. Pandeid shrimp may also ride “piggyback” on hydrozoan medusae (Marliave and Mills, 1993).

There are broad ranges of other types of interactions involving coelenterates. Some, such as bacterial infections, are common but complex and therefore little studied to date. Ectoparasitism by a dinoflagellate on ctenophores and hydromedusae is described by Mills and McLean (1991). Coelenterates may act as intermediate hosts for trematode or cestode parasites which complete their life cycles in fish (Arai, 1988; Purcell and Arai, 2001).

5.6 Growth

5.6.1 Development from the ephyra to medusa stage

Having been released from benthic strobilated polyps, ephyrae are the youngest planktonic life stage of scyphozoan jellyfish, and will develop into mature medusae by feeding and growth. Ephyrae exhibit a basically disc-like morphology. They are characterized by 8 (16 in some taxa) radially extended marginal lappets with disc diameter of 2–5 mm (Russell, 1970; Straehler-Pohl and Jarms, 2010; Holst, 2012) and possess limited swimming and feeding ability compared to medusa, as their marginal lappets generate a smaller feeding current vortex than the medusa's bell (Costello and Colin, 1994; Sullivan *et al.*, 1997) and their narrow, tube-like manubrium is less functional than a medusa's branched and/or elongated oral arms. Hence, availability of proper food is crucial to newly released ephyrae to initiate feeding and attain subsequent development. Dietary information for ephyrae is not extensive, but gastric content examinations and feeding experiments revealed that they feed on a variety of prey such as phytoplankton, ciliates, rotifers, copepods (nauplii, copepodites and adults), hydromedusae, ctenophores and planktonic larvae of various benthic organisms (Olesen, 1995; Sullivan *et al.*, 1997; Båmstedt *et al.*, 2001; Ishii *et al.*, 2004; Møller and Riisgård, 2007). Sullivan *et al.* (1997) investigated prey capture behavior of *A. aurita* s.l. ephyrae in detail, and demonstrated that larger prey swimming continuously at low velocity are most vulnerable, suggesting that slow-swimming hydromedusae may be more important than fast-swimming copepodites and adult copepods, and that continuously swimming rotifers may be more valuable food sources than intermittently swimming copepod nauplii. Moreover, Skikne *et al.* (2009) reported the effectiveness of dissolved organic matter as a nutritional source for ephyrae of *A. labiata*, since it extends their survival when they are kept under starved conditions.

In bloom-forming scyphozoan genera such as *Aurelia, Chrysaora, Cyanea* and *Nemopilema*, the strobilation and subsequent release of ephyrae take place primarily in winter and spring seasons (Toyokawa *et al.*, 2000; Kawahara *et al.*, 2006; Lucas *et al.*, 2012; Thein *et al.*, 2013) when biomass and production rates of micro- and mesozooplankton are generally at an annual minimum level in temperate coastal waters, like the Inland Sea of Japan (Uye *et al.*, 1996; Uye and Shimazu, 1997). The ephyrae in the field are likely to be exposed to starvation due to food scarcity in addition to predation by predators, resulting in their low survival rate as has been commonly demonstrated in newly hatched fish larvae (Hjort, 1926; Blaxter and Hempel, 1963; Bailey and Houde, 1989). Therefore, ephyrae are considered to be a critical stage and their successful survival may be a factor in determining the size of the medusa population.

Starvation resistance in first-feeding ephyrae of *A. aurita* s.l. was evaluated by Fu *et al.* (2014) by determining their point of no return (PNR50), *i.e.*, days of starvation after which 50% of ephyrae died even if they feed. Their PNR50 values were 33.8, 38.4 and 58.6 days at 15, 13, and 9°C, respectively, which are nearly one order of magnitude longer than those of larval marine molluscs, crustaceans and fishes. In a similar experiment conducted for *C. pacifica* ephyrae, the PNR50 was >160 days at 12°C (Kogovsek *et al.*, unpubl.). Such a strong endurance under prolonged starvation, and subsequent recovery upon food availability, is likely an adaptive strategy for schyphozoan ephyrae, at least for these two species, allowing them to survive under scarce food conditions. This further suggests that predation may be a more important factor than food supply to determine the mortality of ephyrae in the field. In the innermost part of Tokyo Bay, Japan, Ishii *et al*. (2004) estimated that the cumulative mortality from newly released ephyrae to young medusa (20 to 28 days old) of the natural *A. aurita* s.l. population reaches approximately 99%. They suspected that this high mortality owes to predation loss rather than to starvation, since the eutrophic Tokyo Bay sustained exceptionally high zooplankton biomass (mean: 382 mg C m^{-3}) during the study period, although the actual predators of ephyrae remain unidentified. Similar field studies to follow the change in abundance corresponding with the developmental stages, from the newly released ephyra stage to the medusa stage, are needed. At the same time, the effects of various abiotic and biotic environmental factors affecting the ecophysiology of ephyrae should also be examined in order to determine causes of the of ephyrae mortality in the field.

5.6.2 Growth rates

As the growth of jellyfish is assumed to be exponential, the specific growth rate, g (day^{-1}), can be calculated by:

$$g = (\text{In}W_t - \text{In}W_0)/\text{t},$$

where W_0 and W_t are the initial and final weights of a jellyfish, and t is time interval (days).

Growth rate in the ephyra stage

A number of laboratory studies have been conducted to determine the growth rates of ephyrae of three scyphozoan genera: *Aurelia, Chrysaora* and *Nemopilema* (Table 5.6.1). Newly hatched *Artemia* nauplii were most commonly used as food sources because their eggs were easy to harvest and because of their high nutritional value for many jellyfish species. Cultured phytoplankton and rotifers, field-caught copepods and benthos larvae, and ground mussel meat were also fed to the ephyrae. It should be noted that the amount of food density used in these laboratory experiments was generally much greater than that encountered in the field.

Food type, amount of food supply and temperature all influenced the growth rate of ephyrae (Table 5.6.1). At a given temperature, *Artemia* nauplii tended to sustain a higher growth rate in *A. aurita* than other foods provided (Båmstedt *et al*., 2001; Møller and Riisgård, 2007, Fig. 5.6.1). It is notable that gelatinous food, *Mnemiopis leiydi*, supported a much higher growth rate of *Chrysaora quinquecirrha* ephyrae than the rotifer *Brachionus plicatilis* (Olesen *et al*., 1996). Båmstedt *et al*. (1999) and Møller and Riisgård (2007) determined the rates of growth of *A. aurita* under excess amounts of food (*Artemia* nauplii or *Brachionus* sp.); the rates increased with increasing temperature within a normal range from 6 to 18°C (Båmstedt *et al*., 1999) and from 4 to 19°C (Møller and Riisgård, 2007) (Fig. 5.6.2).

Table 5.6.1 Growth rates of laboratory-kept ephyrae of different scyphozoan species, under various food and temperature conditions.

Species	Food	Temperature (°C)	Specific growth rate (d^{-1})	Reference
Aurelia aurita	*Artemia* nauplii	Range: 6–18	Range: 0.175–0.345	Båmstedt *et al*., 1999
Aurelia aurita	*Artemia* nauplii	15	0.238	Båmstedt *et al*., 2001
	Calanus finmarchicus copepodites	15, 18	0.066	
	Cryptophyte *Rhodomonas baltica*	15, 18	0.089	
	Small particles of fresh *Mytilus edulis*	15, 18	0.140	
Aurelia aurita	*Artemia* nauplii	15	Max. 0.22	Møller and Riisgård, 2007
	Brachionus sp.	15	Max. 0.23	
	Balanus sp. larvae	15	Max. 0.23	
	Acartia tonsa copepodites and adults	15	Max. 0.13	
	Brachionus sp.	Range: 4–19	Range: 0.05–0.45	
Aurelia labiata	*Artemia* nauplii	Range: 8–21	Range: –0.027– 0.290	Widmer, 2005
Chrysaora quinquecirrha	*Brachionus plicatilis*	23	Max. 0.32	Olesen *et al*., 1996
	Mnemiopis leiydi	23	Max. 0.66	
	Brachionus plicatilis + *Mnemiopis leiydi*	23	Max. 0.70	
Nemopilema nomurai	*Artemia* nauplii	18, 24	0.23	Kawahara and Uye, unpubl.

A similar temperature-dependent increase in growth rate was also observed for *A. labiata* fed with *Artemia* nauplii in excess at different temperatures from 8 to 21°C (Widmer, 2005). When the growth rate of *A. aurita* ephyrae was examined using different prey species (*Artemia* nauplii, *Balanus* sp., Brachionus sp. and *Rathkea octopunctata*) and concentrations (5–115 μg C l^{-1}) at a fixed temperature of 15°C, the *A. aurita* ephyrae increased with increasing food concentration to reach a maximum growth rate of ~0.22 d^{-1}, at about 100 μg C l^{-1} (Fig. 5.6.1, Møller and Riisgård, 2007). The maximum growth rate achieved by ephyrae of the two *Aurelia* species was approximately 0.3–0.4 d^{-1}, but the rate was higher for *C. quinquecirrha* (Table 5.6.1). Such high growth rates may never be accomplished in the field as zooplankton density there is usually much lower than the food supply established in the laboratory. For example, in the Inland Sea of Japan, the ephyrae of *A. aurita* s.l. are released mainly from January to March when mean zooplankton biomass is at an annual minimum, *i.e.*, approximately 2 and 13 μg C l^{-1} for micro- and mesozooplankton, respectively (Uye *et al*., 1996; Uye and Shimazu, 1997). Hence, only when ephyrae can encounter dense enough zooplankton patches can they acquire food sufficient for net growth.

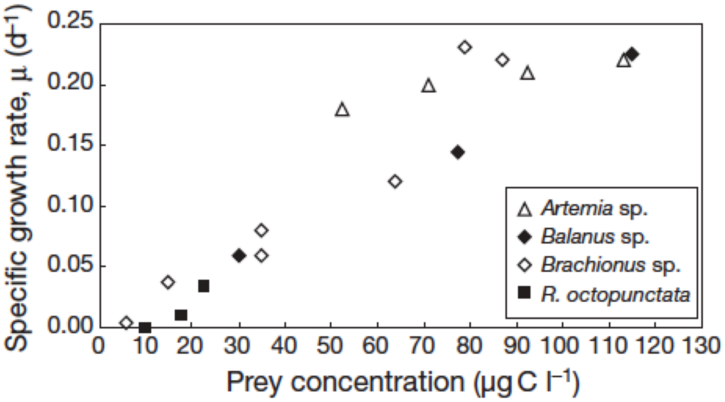


Fig. 5.6.1 Specific growth rate of *Aurelia aurita* in relation to concentration of different food types (*Artemia* sp., *Balanus* sp., *Brachionus* sp. and *Rathkea octopunctata*) at 15°C (from Møller and Riisgård, 2007).

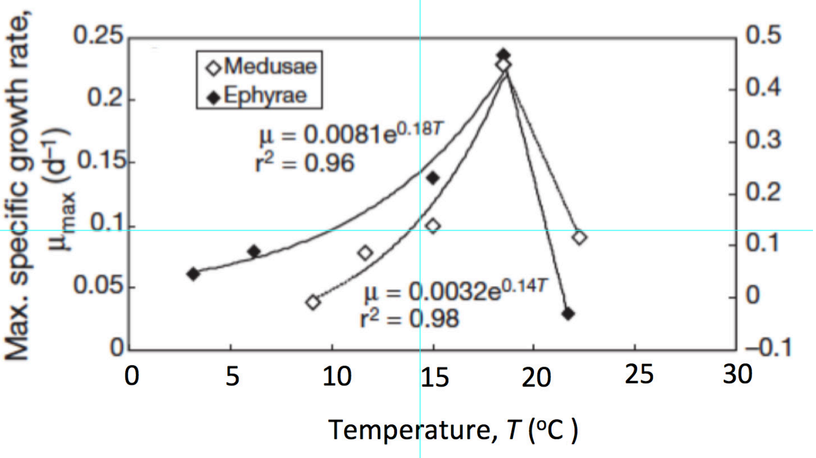


Fig. 5.6.2 Effect of temperature on maximum specific rate of ephyrae (right y-axis) and medusae (left y-axis) of *Aurelia aurita* at (*Artemia* sp., *Balanus* sp., *Brachionus* sp. and *Rathkea octopunctata*) at 15°C (from Møller and Riisgård, 2007).

Growth rate in the medusa stage

Controlled laboratory experiments demonstrated that temperature, prey type and prey density are primary factors to influence the growth rate of medusae of *A. aurita*, as are found in ephyrae (Møller and Riisgård, 2007). Although, under natural conditions, it is difficult to isolate factors to determine the growth rate of schyphozoan medusae, there is an extensive amount of data on their growth rates in the PICES region (Table 5.6.2). Compared to ephyrae, medusae grow more slowly. Their growth is generally most rapid during the young medusa stage prior to sexual maturity, after which the growth is retarded (Hamner and Jenssen, 1974). The growth rates determined in *A. aurita* s.l. in many locations with different ambient temperatures range widely from 0.01 to 0.1 d^{-1}. These rates indicate that their growth may be affected more by ambient food supply than by temperature. The growth rate of *Rhopilema esculemtum* medusae in Chinese coastal waters is much higher (max. 0.17 d^{-1}) than for *A. aurita* because of the higher food supply in Chinese waters. The growth rate of *N. nomurai* in the coastal waters of Japan is much lower than that of *R. esculemtum* in Ariake Bay.

Table 5.6.2 Growth rates of medusae estimated for various scyphozoan species in the PICES region.

Location	Period	Temperature range (^{o}C)	Wet weight range (g)	Specific growth rate (day^{-1})	Reference
Aurelia aurita s.l.					
Urazoko Bay, Japan	May–Aug.	20–28	0.5–26	0.053	Yasuda, 1971
	Sep.–May	8–24	40–400	0.012	Yasuda, 1971
Tokyo Bay, Japan	Mar.–Aug.	12–26	0.018–237	0.066	Omori *et al*., 1995
	Apr.–Aug.	15–28	6.6–422	0.047–0.085	Toyokawa *et al*., 2000
	Apr.–June	15–20	54–269	0.029	Ishii and Tanaka, 2006
Kagoshima Bay, Japan	Feb.–July	14–28	1–587	0.042	Miyake *et al*., 1997
Inland Sea of Japan	Apr.–July	15–25	1–1000	0.049–0.083	Uye and Shimauchi, 2005
Honjo Area, Japan	June–July	24–27	50–90	0.027	Han *et al*., 2009
	May–June	18–22	7–24	0.033	Makabe *et al*., 2012
Mikawa Bay, Japan	Mar.–June	12–22		0.06–0.08	Aoki *et al*., 2012
Sihwa Lake, Korea	July–Aug.	25–30	70–270	0.052	Han *et al*., 2012
Tomales Bay, USA	Mar.–June		0.05–91	0.10	Hamner and Jenssen, 1974
Rhopilema esculemtum					
Minjiang Estuary, China	May–July	20–30	1.2–7,200	0.10	Lu *et al*., 1999
Liaodong Bay, China	June–Aug.	23–28	0.5–7692	0.17	Dong *et al*., 2009
Ariake Bay, Japan	May–Sep.	15–30	0.6–27,000	0.09	Omori, 1981
	June–Aug.	20–29	1,500–26,000	0.057	Uye, unpubl.
Nemopilema nomurai					
Japanese coastal waters	July–Dec.	20–28	7,600–96,300	0.02	Kawahara *et al*., 2006
	July–Nov.	20–28	8,800–08,400	0.03	Uye, unpubl.

Palomares and Pauly (2009) collated published data on seasonal variations in bell diameters of wild jellyfish populations from around the world. These data were fitted to the von Bertalanffy Growth Function, commonly used in fisheries research, to compare the growth parameters, such as the asymptotic body size at which growth becomes zero, and the growth rate of jellyfish to those of fish. They found that the growth rates of jellyfish are largely comparable to those of small fishes such as guppies and anchovies (Palomares and Pauly, 2009).

5.6.3 Degrowth

One of the physio-ecological characteristics demonstrated by gelatinous-bodied medusae and ctenophores is significant degrowth under starvation and regrowth with subsequent feeding. In the North Pacific the phenomenon of degrowth/regrowth has been most extensively examined in the hydromedusan *Aequorea* (Arai, 1986; Arai *et al*., 1989), the scyphomedusan *Aurelia* (Hamner and Jensen, 1974; Uye and Shimanchi, 2005) and the ctenophore *Pleurobrachia* (Fu *et al*., 2014). Even newly released ephyrae exhibit such prominent characteristics, as demonstrated in *A. aurita* s.l. ephyrae (Fu *et al*., 2014). When they were kept in a starved condition, their disc diameter and carbon content decreased by about 30% and

50%, respectively, until the times of their point of no return (33.8, 38.4 and 58.6 days at 15, 12 and 9°C, respectively), and when they were then fed, 50% of them were able to regrow to advanced stages. Degrowth and regrowth are also common in the medusa stage, as demonstrated in *A. aurita* s.l. in Tomales Bay, California (Hamner and Jensen, 1974). When batches of medusae of three different bell diameters (small: 3–5 cm, medium: 8–9 cm, large: 10–11 cm) were starved at 16–18°C for various periods up to 100 days, they shrank with starvation duration to <2 cm bell diameter. When they were then fed, they showed enough recovery to grow larger than their initial size at the start of the experiment, except for extremely shrunken individuals of <2 cm bell diameter, which failed to regrow. These facts indicate that the growth rate of the natural jellyfish population may change spatially as well as temporally according to food supply conditions in the field. However, after seasonal spawning, senescent individuals lose a significant amount of body mass but can survive for several months before they die. Such a seasonal pattern was observed, for example, in *A. aurita* s.l. in the Inland Sea of Japan, where their average body weight was largest in July, a peak spawning month, and decreased rapidly thereafter until they died in November (Uye and Shimanchi, 2005).

5.6.4 Longevity in plankton stages

In temperate waters, many hydrozoan and scyphozoan species start their planktonic life as newly released ephyrae in spring, mature sexually by fall, and undergo senescence after spawning to undergo morphological degradation. Hence, the time of their planktonic life is usually less than a year (Mills, 1993; Miyake *et al*., 1997) although many exceptions exist. For example, *A. aurita* s.l. medusae can overwinter in Urazoko Bay and Tokyo Bay, Japan, attaining a total life span of 14–15 months (Yasuda, 1971; Omori *et al*., 1995). In Roscoe Bay, west coast of Canada, *Aurelia labiata* can live for 2 years and more (Albert, 2005; Albert and Walsh, 2013). In boreal waters such as the Bering Sea, the longevity of *Chrysaora melanaster* in the plankton stage may last for multiple years, as large medusae appearing in spring may be overwintered individuals (Brodeur *et al*., 2008). Multi-year life spans have also been reported for warm water scyphozoans, for example, *Pelagia noctiluca* can live as long as 500 days at 18°C in the laboratory (Lilley *et al*., 2014).

6 Ecological and Socio-Economic Impacts of Jellyfish

Richard Brodeur[1], Lucas Brotz[2], Jennifer Purcell[3] and Shin-ichi Uye[4]

[1] Northwest Fisheries Science Center, Hatfield Marine Science Center, National Marine Fisheries Service, NOAA, Newport, Oregon, USA
[2] Sea Around Us Project, University of British Columbia, Vancouver, British Columbia, Canada
[3] Shanonn Point Marine Center, Western Washington University, Anacortes, Washington, USA
[4] Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Japan

6.1 Introduction

Speculation continues about whether jellyfish populations are increasing worldwide, at least in part due to anthropogenic degradation of the environment (*e.g*., Purcell *et al*., 2007; Purcell, 2012; Condon *et al*., 2012). There is mounting evidence that populations fluctuate with climatic cycles and that temperate species may increase their abundances, and spatial and seasonal distributions in a warming climate (Purcell, 2005). "Fishing down the food web" reduces piscivorous fish (Pauly and Palomares, 2001), which favors zooplanktivorous fish that are heavily fished to produce oil and meal for aquaculture feeds (Tacon and Metian, 2009); the catches of forage fish increased almost ninefold between 1950 and 2006 (http://www.seaaroundus.org). This further "fishing down" removes competitors of jellyfish, possibly increasing their success (*e.g*., Purcell *et al*., 2007; Purcell, 2012).

Jellyfish are usually regarded as harmful to humans, primarily due to stings, but they are also beneficial to humans in many ways. One of the most positive aspects of jellyfish is their edibility (Kingsford *et al*., 2000; Omori and Nakano, 2001). Approximately 900,000 tons of jellyfish, primarily rhizostomes, are commercially harvested around the world (Brotz, 2016) and consumed as traditional food in Asian countries. Jellyfish provide other benefits to humans through their ecological roles in marine ecosystems. For example, Cnidaria and Ctenophora, which originated during the Cambrian period (Hagadorn *et al*., 2002; Chen *et al*., 2007), have survived for more than 500 million years as the most ancient multicellular organisms on Earth. Adapting to various environmental conditions, they are now ubiquitous and play pivotal roles in marine ecosystems. Hence, jellyfish and their ecosystems provide a variety of benefits to humankind, or "ecosystem services", defined by the Millennium Ecosystem Assessment (2005), which are divided into four categories: regulating, supporting, provisioning, and cultural, as summarized in Table 6.1.1 (see also Doyle *et al*., 2014; Graham *et al*., 2014; Lucas *et al*., 2014, for reviews).

Table 6.1.1 Summary of the ecosystem services provided by jellyfish in various parts of the world.

Service category	Specific services	References
Regulating	1. Climate regulation through carbon sequestration (*e.g.*, jellyfish falls, salp fecal pellet production)	Madin *et al.*, 2006; Lebrato *et al.*, 2012
	2. Disease and pest regulation (*e.g.*, predation of potentially harmful *Mnemiopsis leidyi* by *Beroe ovata*)	Shiganova *et al.*, 2001; Kideys, 2002
	3. Biodiversity regulation (*e.g.*, control of fish populations by eating their eggs and larvae to prevent from overly dominant fish species)	Boero *et al.*, 2008; Pauly *et al.*, 2009
Supporting	1. As habitats and/or refugia for fish (*e.g.*, walleye pollock, Atlantic cod, haddock, mackerels)	Purcell and Arai, 2001; Masuda, 2009
	2. As hosts for parasites (*e.g.*, hyperiid amphipods, barnacles, copepods, isopods, shrimp, crabs) and symbiotic zooxanthellae	Dawson and Hamner, 2003; Ohtsuka *et al.*, 2009
	3. As prey for other jellyfish (*e.g.*, *Cyanea* spp., *Beroe* spp.), fish (*e.g.*, sunfish, chum salmon), reptiles (*e.g.*, leatherback sea turtles) and birds	Arai, 2005; Houghton *et al.*, 2006
	4. As predators of a variety of zooplankton (*e.g.*, ciliates, copepods, euphausiids, fish eggs and larvae, other jellyfish) and nekton (fish)	Purcell, 1989, 1997; Boero *et al.*, 2008
	5. Nutrient cycling through excretion, mucus production, sloppy feeding, and biogenic mixing due to water displacement by swimming	Pitt *et al.*, 2009; Katija and Dabiri, 2009; Condon *et al.*, 2011
Provisioning	1. Food resources, particularly rhizostome species traditionally consumed in many Asian countries	Omori and Nakano, 2001
	2. Source of useful biochemical compounds (*e.g.*, green fluorescent protein (GFP), collagen, mucin, nematocyst toxins)	Zimmer, 2009; Addad *et al.*, 2011; Leone *et al.*, 2013
Cultural	1. Generation of ecotourism (*e.g.*, Jellyfish Lake in Palau)	Dawson *et al.*, 2001
	2. Possession of aesthetic value (*e.g.*, aquarium exhibition, artistic works)	Graham *et al.*, 2014
	3. Facilitation of environmental education to the public (*e.g.*, volunteer identification and counting of jellyfish stranded on beaches)	Silvertown, 2009

Recent enhancement of human activities have cumulatively affected the world's oceans resulting in significant loss of ecosystem health, particularly in coastal waters along highly populated areas such as East Asia and Europe (Halpern *et al.*, 2008). Human-induced environmental and ecosystem deteriorations, *e.g.*, global warming, eutrophication, deoxygenation, marine construction, loss of biodiversity, and decrease in fish stock may have worked as drivers leading to the increase of jellyfish populations in recent decades (Purcell *et al.*, 2007; Richardson *et al.*, 2009; Uye, 2011; Brotz *et al.*, 2012) although it is argued that the there is no robust evidence for a global increase of jellyfish populations (Condon *et al.*, 2013). Unless proper countermeasures are to be taken to restore coastal ecosystem health, jellyfish populations are likely to proliferate more because of their opportunistic nature, which may lead to further increase of adverse jellyfish impacts on intrinsic ecosystem services provided by the ocean that humans decisively depend on. In this section, the ecological and socio-economic impacts of jellyfish will be reviewed.

6.2 Jellyfish fisheries

Jellyfish are considered traditional food in China, where they have been caught and eaten for more than 1,700 years (Omori and Nakano, 2001). Consumption is also popular in Japan, Korea, and several other countries in Southeast Asia. All PICES member countries have attempted jellyfish fisheries, with varying degrees of success (see below). Currently, there are at least 20 countries around the world fishing for jellyfish (with many more that have explored test fisheries), resulting in contemporary global landings on the order of at least 900,000 tons annually (Brotz, 2016). Jellyfish are most often caught using dip-nets; however, a variety of other gears may be employed, including set nets, gill nets, drift nets, seines, trawls, weirs, and hooks. Target species are primarily rhizostomes but occasionally semaeostomes, coronates, or even cubozoans are consumed. In a few coastal regions jellyfish may be eaten fresh, but normally jellyfish undergo initial processing within hours of being caught. Processing is a stepwise procedure that often takes weeks, and involves soaking in different mixtures of salt and alum (usually potassium aluminum sulfate). Processing methods may vary by region, species, and market preferences, but primarily serve to partially dehydrate the jellyfish, ultimately resulting in the characteristic crunchy texture that is desirable for edible jellyfish (Hsieh *et al*., 2001). Depending on the species and processing method used, the final product usually weighs somewhere between 7 and 30% of the landed wet weight (Wootton *et al*., 1982; Huang, 1986; Hsieh *et al*., 2001). Processed jellyfish is typically sliced, soaked and rinsed several times, and sometimes scalded or blanched before serving as part of a simple salad or as an ingredient in more elaborate dishes. More recently, ready-to-use products have also been developed, which are edible straight from the package. Despite the long list of purported health benefits from consumption of jellyfish (*e.g*., Hsieh *et al*., 2001; You *et al*., 2007), there are concerns related to the consumption of aluminum due to the alum used during processing.

As mentioned, China has the longest history of catching jellyfish, and is also the world's largest producer, primarily targeting two species: *Rhopilema esculentum* and the giant jellyfish, *Nemopilema nomurai*. *Rhopilema esculentum* is the most valuable species of edible jellyfish, and is also the focus of aquaculture operations in China, whereby jellyfish are raised in large saltwater ponds. Declining abundance of this species in the wild, likely due to overfishing (Dong *et al*., 2014), prompted the study and development of a hatchery program in the 1970s and 1980s, and now hundreds of millions of ephyrae are reared in laboratories and released into coastal waters each year (You *et al*., 2007; Dong *et al*., 2009, 2014). While there were early reports of success of this program (You *et al*., 2007; Dong *et al*., 2009), catches of *R. esculentum* have declined recently despite increased hatchery output, and effort targeting *N. nomurai* has increased (Li *et al*., 2014). Hundreds of thousands of tons of both species are now landed annually, but *N. nomurai* now makes up the majority of the catch. Other species are also landed for food in China, including *Lobonema smithi*, *Lobonemoides gracilis*, *Rhopilema hispidum*, and *Cyanea nozakii*; however, the catches of these species are presumably quite small in comparison to the two aforementioned species.

Japan also has a history of targeting jellyfish, but has never explicitly reported jellyfish catches to the Food and Agriculture Organization of the United Nations (FAO), which compiles global fisheries statistics. Omori (1981) notes that there are records of jellyfish fishing in the Inland Sea of Japan dating back to the late 1800s. Additional reports also point to fishing for *N. nomurai* off the Hokuriku coast, located on the central part of Honshu, *R. esculentum* along the coasts of western Japan, as well as jellyfish fishing in Wakasa Bay, Mutsu Bay, and off Tōhoku (Omori, 1978, 1981). Most of these reports are from the 1970s, and it is unclear if jellyfish are still harvested locally in these regions today. One region where fishing for jellyfish has persisted is the Ariake Sea, the largest bay in the southern island of Kyushu. Catches primarily consist of *R. esculentum*, and to a lesser extent, *R. hispidum*. Historically, catches were estimated to total approximately 1,000 tons annually (Morikawa, 1984), but processing became more industrialized in the late 1970s and catches swelled to more than 10,000 tons (Omori, 1981). However, catches declined through the 1980s, and have only recently increased to the magnitude seen at the end of the 1970s.

Korea also does not report explicit catches of jellyfish to FAO; however, Omori (1981) reports fishing for jellyfish occurred historically in southwestern Korea, near Mokpo, insinuating that fishing for jellyfish in Korea may actually extend back centuries, rather than just decades. More recent fishing for jellyfish in Korea occurs along the southwestern coast near Muan and Gunsan (Omori, 1981), as well as farther north near Ganghwa Island in Incheon. Fishing typically occurs between September and November, with the majority of the catch destined for export to China.

Russia has a nascent jellyfish fishery in the Far East. Chronicled by Yakovlev *et al*. (2005), *R. esculentum* was apparently rare along the Primorsky Coast prior to 1999. Thereafter, it arrived in Peter the Great Bay in large abundances, presumably carried there by shifting currents, as other rare marine species started showing up around the same time. Approximately 2,000 tons were landed in 2000, followed by 346 tons in 2001. According to FAO, catches have continued since 2003 at <1,000 tons annually.

Canada has attempted fisheries for jellyfish on both the Atlantic and Pacific coasts (Sloan and Gunn, 1985; DFA, 2002); however, neither fishery was developed, predominantly due to the fact that the target species was *Aurelia* spp. Semeaostome jellyfish do not typically produce the desired crunchy texture typical of edible jellyfish, and therefore, lack significant market demand.

The U.S. also had a fishery for jellyfish in the Pacific, but instead of catching jellyfish for food, the hydromedusan *Aequorea victoria* was being targeted in Puget Sound for research on bioluminescence. The investigations eventually led to the discovery of "green fluorescent protein" (GFP), an invaluable genetic marker for biotechnology. In 2008, the Nobel Prize in Chemistry was awarded for the discovery and development of GFP. GFP is now synthesized in the laboratory, so *A. victoria* has not been targeted since the 1990s. The U.S. also has established jellyfish fisheries for the cannonball jellyfish *Stomolophus meleagris* on the Atlantic coast and in the Gulf of Mexico. A total of approximately 5,000 tons of *S. meleagris* are caught in the waters off Florida and Georgia each year, which are then processed and exported to Asia for food.

As jellyfish populations appear to be increasing in many coastal areas of the world (Brotz *et al*., 2012), it has been suggested that society should look for new ways to exploit them (*e.g*., Purcell *et al*., 2007; Richardson *et al*., 2009). This strategy is unlikely to solve our jellyfish problems, and indeed, may create new ones (Gibbons *et al*., 2015). Nonetheless, it is likely that jellyfish fisheries will continue to expand in areas where rhizostome jellyfish are abundant, especially as more traditional seafood stocks continue to decline.

6.3 Food web and modeling

Although there is a substantial number of detailed food web models available for many of the Large Marine Ecosystems of the world, very few of them have explicitly included gelatinous zooplankton and if they do, they are often aggregated into a single group (Pauly *et al*., 2009) which does not capture the diversity of predator–prey interactions in this taxonomically-diverse assemblage. One of the first papers to examine the effects of jellyfish in a coastal ecosystem was an examination of the impacts large blooms have had on the Oregon upwelling ecosystem (Ruzicka *et al*., 2007). Using mass balanced Ecopath models parameterized for the pelagic ecosystem from numerous field studies, Ruzicka *et al*. compared the seasonal food consumption of large jellyfishes (primarily *Chrysaora fuscesens*) to that of forage fishes and other major components of the ecosystem. They found that jellyfish can be the major consumers of zooplankton during the late summer months and can exert substantial top-down effects on several zooplankton groups. They also found that during the time of peak jellyfish abundance (summer), they pass on only 2% of their biomass to higher trophic levels whereas forage fishes pass along 17% of their biomass to higher levels (Ruzicka *et al*., 2007).

Subsequent work in this system quantified the relative contribution of energy up the food web (reach) and the direct and indirect impact of a consumer on lower trophic levels (footprint) as ecosystem metrics that can be used for management (Brodeur *et al*., 2011; Ruzicka *et al*., 2012). The previous top-down driven Ecopath model was inverted (Steele and Ruzicka, 2011) and turned into an end-to-end model where hypothetical scenarios could be changing the flow to or from key nodes in the system. As an example, increasing the energy flow to jellyfish without increasing the overall productivity of the model led to a substantial decline in the productivity of forage fish in this system (Fig. 6.3.1).

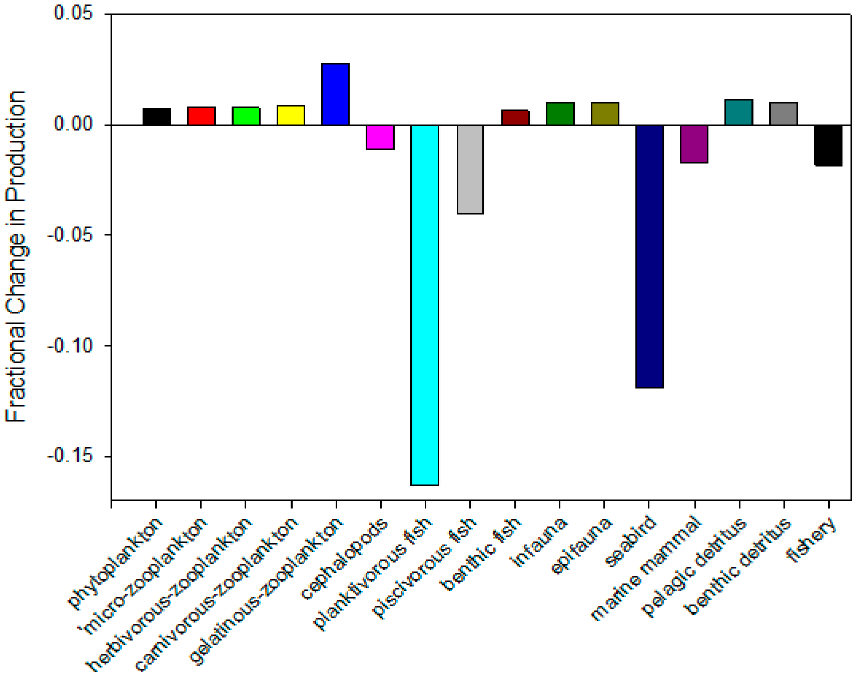


Fig. 6.3.1 Output (fractional change in production of each trophic group) of a scenario where the amount of food going to jellyfish is increased 5% compared to the base model, without any increase in the total productivity of the model (from Brodeur *et al*., 2011).

These end-to-end models have been extended to examine interannual variability in the relative roles that jellyfish, forage fish and euphausiids play in the Northern California Current (NCC) driven by nutrient input rates (Ruzicka *et al*., 2012). These results indicate that jellyfish have a much greater footprint and smaller reach than forage fishes, especially euphausiids, in this system and were thus a much less efficient node in the food web. Continued work comparing the NCC to other North Pacific ecosystems, including the Gulf of Alaska (Ruzicka *et al*., 2013) and the Bering Sea (Robinson *et al*., 2014), has found that jellyfish are more important in the NCC than the other two systems. A more recent application of the model demonstrated that juvenile salmon, when they first enter coastal waters, may also be heavily impacted by increases in jellyfish biomass in the NCC (Ruzicka *et al*., 2016).

6.4 Economic impacts of jellyfish blooms

6.4.1 Damage to fisheries

Because of their propensity to form dense aggregations, some large scyphozoan species have undoubtedly hampered fisheries for many years, and fishermen may have accepted such occurrences as unavoidable natural phenomena. In several fishing communities around the Inland Sea of Japan, there was an old custom called “kurage matsuri” meaning “jellyfish festival”, when jellyfish appeared abundantly in the fishing grounds. During this period, fishermen gave up going fishing but met at a nearby shrine or Buddhist temple to pray for a swift jellyfish disappearance. This custom persisted until the end of the last century.

The paper by Kishinouye (1922), which described the damage to set nets along the Hokuriku District, central Honshu, by the massive bloom of *N. nomurai* in 1920, might be one of the earliest scientific reports on the nuisance of jellyfish to fisheries, and similar incidences have been reported frequently since the 1990s, particularly in Asian countries (*e.g*., Purcell *et al*., 2007; Dong *et al*., 2010; Kim *et al*., 2012). Nowadays, jellyfish impacts on fisheries occur worldwide, *e.g*., in North and South Americas (Graham *et al*., 2003; Nagata *et al*., 2009; Quiñones *et al*., 2013; Conley and Southward, 2015), Europe (Nastav *et al*., 2013; Tiller *et al*., 2015), Africa (Lynam *et al*., 2006), and the Middle East (Daryanbard and Dawson, 2008).

One of the most serious cases is attributed to the massive blooms of *N. nomurai* in Japanese and Korean coastal waters (Uye, 2008; Kim *et al*., 2012). The nuisance consists of: 1) clogging and bursting fishing nets, 2) decreasing fish catch, 3) killing and spoiling fish, 4) stinging fishermen as they try to remove jellyfish from their nets, 5) increasing the time and labor effort during the removal of medusae from the nets, and 6) causing fishing boats to capsize. In 2005, the number of complaints from Japanese fishermen reached over 100,000 of which 60% were related to reduced catch, value of catch, and suspension of operations, 30% to increased labor time to remove fish, and 10% to net damage. The nation-wide monetary loss was estimated to be approximately 30 billion JPY, or 250 million USD (Uye, 2008). In Korea, economic losses based on decreased fish catches and value due to jellyfish blooms between 2006 and 2009 were estimated to be 68.2 –204.6 million USD, depending on the period of jellyfish occurrence (Kim *et al*., 2012). In both countries, set net fisheries are most susceptible to jellyfish aggregations and hence, the economic damage is largest among various net fisheries. Around the Japanese coast there are over 4,000 set nets of various scales and approximately half of them are located in regions where *N. nomurai* are present. A large-scale set net, consisting of a 2 to 5 km-long leading net heading into a large chamber and a series of progressively smaller trapping nets, provides a livelihood for 10–30 fishermen (annual revenue: 0.8–2.5 million USD). In 2005, the operation of many set nets was suspended, and fishermen were obliged to temporarily refrain from working.

The economic impact of jellyfish upon fisheries was examined in the northern California Current system off Oregon, where *Chrysaora fuscescens* is densely distributed (Suchman and Brodeur, 2005; Brodeur *et al*., 2008), by mail surveys to local fishers (Conley and Southward, 2015). Of the total respondents, 67% reported that jellyfish reduced their seasonal revenue, and the estimated economic impact of jellyfish on salmon and pink shrimp fishers was over 650,000 USD in peak jellyfish season in 2012. According to fishers' reports, the jellyfish impact is not solely upon net fisheries, but also upon hook and line fisheries. In the latter case, jellyfish foul gears, shorten fishing time, reduce catch, and force fishers to relocate. In the northern Gulf of Mexico, the non-indigenous large rhizostome *Phyllorhiza punctata* bloomed massively in 2001, resulting in an estimated 10 million USD loss to the local shrimp fishery (Graham *et al*., 2003).

The Peruvian anchovy fishery is one of the largest single-species fisheries in the world. Annual catch is largely affected by the El Niño and La Niña oscillation, but the catch is also affected seasonally by the large semaeostome *Chrysaora plocamia* (Quiñones *et al*., 2013). This jellyfish species blooms in summer, and is often caught in the seine nets as by-catch. In the summer of 2008–2009, *C. plocamia* accounted for >10% of the catch by weight in 10% of the hauls, and >30% of the catch in 5% of the hauls. Processing factories deducted the weight of jellyfish when the by-catch exceeded 13%, and refused to receive the catch if jellyfish accounted for >40%. The economic losses due to jellyfish in 2008–2009 were estimated to be approximately 200,000 USD in only 35 days of fishing. This economic loss could substantially increase during warm periods such as El Niño, when the *C. plocamia* population might increase (Quiñones *et al*., 2013).

A traditional fishery for the edible jellyfish *R. esculentum* in Liaodong Bay, China, was hampered by the bloom of *C. nozakii* in 2004. Because of predation of and competition for available food with *C. nozakii*, the catch of *R. esculentum* in that year declined to 20% of the regular annual catch, resulting in a direct economic loss of approximately 70 million USD (Ge and He, 2004).

6.4.2 Damage to aquaculture

The negative interactions between jellyfish (primarily cnidarians – those with stinging cells) and fish in aquaculture appear to be an increasing problem through the intensification of aquaculture operations in many coastal areas worldwide. Over the last three decades there have been numerous fish kill events or health problems in marine-farmed fish that have been associated with jellyfish (Purcell *et al*., 2007; Graham *et al*. 2014). The majority of problems have occurred with marine-farmed salmonids in northwestern Europe (Rodger *et al*., 2011a). Nevertheless, aquaculture operations in other regions such as Asia, North America, and Australia have also been affected (Yasuda, 1988; Willcox *et al*., 2008; Rodger *et al*., 2011a). Although large-scale jellyfish blooms can sometimes be the obvious cause (in the case of conspicuous scyphomedusae), often problems are associated with small transparent species. A lack of sampling and investigation around these types of events has previously inhibited the identification of the causative agents (Cronin *et al*., 2004). Furthermore, while mass mortality events are commonly reported in the literature and the media, lower level health problems are very poorly reported despite the scale of the problems in some regions (Rodger, 2007).

Almost all of the initial gill damage caused by cnidarians is due to their stings. Cnidarian jellyfish are characterized by having millions of microscopic stinging cells, primarily in their tentacles. Inside the cell is a specialized stinging capsule called a nematocyst (most 10–20 µm long) which contains a coiled, harpoon-like hollow tubule, often armed with spines. Nematocysts can be triggered by mechanical or chemical stimulation. Toxins can be injected from the nematocyst into the prey to immobilize them. Each jellyfish can have a variety of nematocysts that differ in size, shape, and toxicity among species. When a nematocyst fires, mechanical damage is caused when the tubule penetrates the tissue, as well as toxic damage from the activities of the enzymes, neurotoxins, myotoxins, and hemolytic compounds contained within (Mariottini and Pane, 2010). As such, nematocysts are especially damaging to delicate fish gills.

Gill disorders (damage to the gill arch and filaments caused by pathogens and parasites) are emerging as one of the most serious causes of mortality in marine-farmed salmonids (Rodger, 2007), with an average of 12% mortality of farmed fish recorded annually from Irish fish farms (Rodger and Mitchell, 2005). In temperate regions where salmonids are cultivated, gill disorders typically occur in late summer (giving rise to the term "summer syndrome"). Information on the interactions with other fish species is even scarcer. Gill disorders are thought to be multifactorial, often caused by a primary attack from agents like jellyfish, leaving the gills open to secondary bacterial infections which exacerbate the problem (Rodger *et al*., 2011a). Although gill disorders can be caused by a variety of agents, *e.g*., jellyfish, phytoplankton, amoeba, parasites, bacteria, and viruses, the type of damage exhibited by the gills is observed with a limited number of responses, *i.e*., hemorrhage, necrosis, edema. Whilst some causative agents can be easily diagnosed by microscopy or histopathology, others cannot. With respect to jellyfish-mediated damage, recent monitoring studies and experimental trials have significantly increased the knowledge on the pathogenesis of the disorder (Baxter *et al*., 2011a,b).

Several types of jellyfish have been previously linked to fish kill events and gill damage in marine-farmed fish, including hydromedusae, scyphomedusae, siphonophores, and ctenophores. Hydromedusae are a diverse group (>800 species worldwide), most of which are <1 cm in size and transparent, thereby going mostly unnoticed by humans. Because of their small sizes, they can pass through nets and some directly into the opercula of the fish. Many species produce medusae asexually from the hydroid stage, which lives attached to hard surfaces, including aquaculture structures. Other species are holoplanktonic and lack an attached benthic stage, *e.g., Solmaris corona*; still other species, *e.g*., *Ectopleura larynx* syn. *Tubularia larynx* produce swimming larvae, but not medusae.

Ephyrae and small medusae of the common jellyfish *Aurelia aurita* s.l., are thought to have caused huge losses of farmed fish in Norway and Scotland in the mid-1990s through suffocation (Båmstedt *et al*., 1998). Incidents of *A. aurita* s.l. causing mortalities of farmed fish in Tasmania and Asia also exist (Yasuda, 1988; Willcox *et al*., 2008). Nevertheless, until recently, the potential damage caused by *A. aurita* s.l. has been underestimated. Large aggregations of the specie*s* are a common occurrence around aquaculture sites in northwestern Europe, though problems associated with them often go overlooked due to their mild sting to human skin. This may not be the case for more delicate fish gills. Mitchell *et al*. (2011) documented the pathological damage to Atlantic salmon caused by such an aggregation at a salmon farm in Ireland. The authors were the first to show intravascular hemolysis combined with multifocal hemorrhage and lamellar thickening of the gills over the duration of the event (~3,000 mortalities in the first week after the occurrence of *A. aurita* s.l.) and damage persisted at two months after the event. Controlled challenge experiments where Atlantic salmon were exposed to *A. aurita* s.l. also described the pathogenesis of the gill damage caused by this species (Baxter *et al*., 2011b). The damage presented as widespread multifocal hemorrhage, necrosis and fusion of the lamellae. There was also a lag in the peak of the damage after the jellyfish had been removed and a delayed inflammatory response. As with the field observations, the damage was still present three weeks after the challenge. Moreover, up to an 85% reduction in gill cell viability was observed from *in vitro* experiments where an assay of rainbow trout gill cells was exposed to toxins extracted from *A. aurita* s.l. and *C. capillata* stinging capsules (Helmholz *et al*., 2010).

A further threat to the finfish aquaculture industry is posed by the hydroid stage of hydrozoans. These sessile animals are known to rapidly and extensively foul aquaculture structures (pontoons and netting) (Carl *et al*., 2010). Before now, it was unknown whether hydroids (which also possess stinging cells) affect farmed fish health and play a role in gill disorders (Rodger *et al*., 2011a). The risk of damage caused by biofouling hydroids was briefly mentioned in an examination of clubbing and gill necrosis syndrome in Atlantic salmon in Tasmania (Clark *et al*., 1997). Some hydroid species, such as *Ectopleura larynx*, have become the dominant fouling organisms of the fish farming industry in Norway, where they cause problems by reducing water flow and quality (Guenther *et al*., 2009; Carl *et al*., 2010). This fast-growing species is common and abundant in many European coastal waters (Browne, 1897; Boero and Fresi, 1986; Östman *et al*., 1995; Galea, 2007) and is now becoming prevalent on Irish finfish farms.

Organic farms, which are not permitted to use copper-based anti-foulants that other farms use (IOFGA, 2006), have to clean the nets every 3–4 weeks during the peak period of hydroid growth. *In situ* net washing is an increasingly common means to deal with such biofouling. This practice uses rotating discs that jet-wash the nets at high pressure (Guenther *et al*., 2010). This blasts pieces of hydroids into the water that then can damage the fish. After the first net wash of the production cycle, hydroids can grow at an even faster rate than before because remnants can remain on the net (Guenther *et al*., 2010). However, efforts to investigate this potential problem and the effects of net washing have been neglected until recently. Baxter *et al*. (2012) quantified the rapid growth of the biofouling hydroid *E. larynx* on aquaculture nets and used experimental challenge trials to identify possible damage they can cause to fish in aquaculture. Fish were exposed to hydroid-fouled nets and to loose hydroids, to simulate the process of net washing. Indeed, the hydroids caused gill damage to Atlantic salmon smolts in both treatment groups over the duration of the experiment. This was visible under histopathology as focal areas of epithelial sloughing and necrosis. Such damage has been linked to lethargy and decreased appetite in farmed salmon (Rodger *et al*., 2011b). Some medusa-producing hydroids are known to live on aquaculture structures and nets (Chaplygina, 1993) although little documentation exists. *Obelia* spp. are ubiquitous in harbors globally and produce great numbers of 1-mm medusae that might damage fish gills, although no direct evidence yet exists.

Aquaculture operations also can have several potentially beneficial effects on jellyfish populations at local scales (Purcell, 2005). Lo *et al*. (2008) discussed how increased nutrients around the farms, due to excess fish food and waste products, could create eutrophic conditions that may favor jellyfish over fish, such as smaller zooplankton that are less beneficial foods for fish and decreased dissolved oxygen and water clarity (Arai, 2001; Purcell *et al*., 2007). Furthermore, the structures of aquaculture facilities (*e.g*., cages, pontoons, and feed barges) may restrict water flow which could act to retain medusae, as well as provide substrates for the benthic stages (Båmstedt *et al*., 1998; Lo *et al*., 2008). Problems associated with jellyfish are likely to arise in all areas of finfish production where jellyfish are abundant (Rodger, 2007). Many highly productive aquaculture operations in regions such as Asia, northwestern Europe, Australia, and South America have already been affected (Båmstedt *et al*., 1998; Doyle *et al*., 2008; Lo *et al*., 2008; Willcox *et al*., 2008). Therefore, the global expansion of the aquaculture industry is of increasing concern due to its potential to enhance jellyfish populations. In the future, this could mean more frequent and significant losses of finfish as a result of interactions with jellyfish.

6.4.3 Damage to coastal power plants and other facilities

Approximately 40% of the world's human population lives within 100 km of the coast. Increased demand for electricity has been met by construction of power plants along the coast, since large amounts of seawater are required to cool their condensers. Hence, the concurrent jellyfish ingress to the plants is unavoidable. Jellyfish became problematic for thermal power plants along Tokyo Bay in the 1960s (Kuwabara *et al*., 1969; Matsueda, 1969), and brought about the complete shutdown of a plant that led to the blackout of the Tokyo metropolitan area in 1972. Since then, the power stations have installed a series of nets and air-bubble generators in front of the water intakes to avoid clogging by jellyfish. At present, there are 12 major power plants along the coast of Tokyo Bay, and a sudden ingress of a large abundances of *A. aurita* s.l. is always a threat to their operation, especially in summer, which is the peak season for both electricity demand and the medusa population. In Mikawa Bay, there were only a few such incidences each year until 1972, but there was a marked increase (up to 29 incidences) in 1973, when a new, large station launched. Hence, the numbers of incidences due to jellyfish clogging might be associated with the increase in plant operation capacity, as well as the increase of the jellyfish population. As Japanese power companies are reluctant to make public the actual damage (or monetary loss) by jellyfish aggregations and/or amount of jellyfish removed from intake screens, they invested significant funds for the installation of jellyfish deterrent and removal apparatus (*e.g*., screens, air bubble generators, ladders, conveyers, reservoirs, and monitoring and alarming systems) and paid extra money for their removal and damping them when a sudden ingress of a large aggregation of jellyfish occurred.

In Korea, the first shutdown of a power station due to jellyfish ingress took place in 1996 at Uljin Nuclear Power Station. Since then, a number of shutdowns and decreases of power production have occurred (Korean Nuclear Power Plant Operational Performance Information System, http://opis.kins.re.kr). In China, jellyfish ingress has also become a serious problem for power stations along the Bohai and Yellow Seas. For example, in July 2008, over 4,000 tons of jellyfish were cleaned up from the intake screens of a coastal power plant in Qinhuangdao, Hebei Province (Liu, 2008). In August 2008, 20–50 tons of jellyfish were also removed at a power plant in Weihai, Shandong Province (Dong *et al*., 2010).

Interference with power plant operation by jellyfish has spread worldwide (Purcell *et al*., 2007; Graham *et al*., 2014; Lucas *et al*., 2014) so that we often encounter news of such incidents on the Internet, including a very special case that the American warship, the USS *Ronald Reagan*, was negatively affected by jellyfish clogging the ships condensors (http://www.freerepublic.com/focus/news/1566004/posts). Desalination plants, which require a large amount of seawater, are also susceptible to jellyfish ingress (Daryanbard and Dawson, 2008).

6.4.4 Damage to tourism

Coastal tourism is one of the largest sectors of the economy in numerous tropical and subtropical regions, as well as the Mediterranean area. However, in many of these areas, there are jellyfish species with venomous nematocysts, causing severe stings to many swimmers, and even resulting in fatalities (Fenner and Williamson, 1996; Burnett, 2001; Purcell *et al*., 2007). Severe jellyfish stings occur most frequently in northern Australia, Thailand, the Philippines, and other Pacific nations, where the cubozoan *Chironex fleckeri* can cause cardiac and respiratory arrest leading to death in severe cases, as well as *Carukia barnesi* which gives rise to the infamous Irukandji syndrome (Fenner and Williamson, 1996; Fenner and Hadock, 2002; Fenner *et al*., 2010). There were at least 67 fatalities due to *Chironex* stings in Australia alone between 1984 and 1996 (Fenner and Harrison, 2000), and 20–50 fatalities annually as a result of jellyfish stings in Malaysia and the Philippines (Fenner *et al*., 2010). In the Mediterranean, the mauve stinger *Pelagia noctiluca*, which has been increasing in recent years (Kogovšek *et al*., 2010), is the most common jellyfish responsible for stings. Hence, when this species appears abundantly along resort beaches, stinging often takes place at epidemic levels. For example, there were several thousand sting reports each year from the French Riviera alone, and in July 2008, French emergency services received more than 500 calls in one day (Bernard *et al*., 2011). Beaches infested with the aforementioned jellyfish species are undoubtedly detrimental to tourist appeal, which causes tourists to seek alternative destinations. Therefore, direct economic losses due to jellyfish in the tourism industry may be extremely large, and these losses are expected to grow as human populations and recreational activities continue to increase along the coasts.

In the PICES region, particularly temperate East Asia, negative impacts of jellyfish on tourism are comparatively much smaller. However, severe stings, including fatal cases, have been reported for various hydrozoans (*e.g*., *Gonionemus*, *Olindias*, and *Physalia*), scyphozoans (*e.g*., *Aurelia*, *Chrysaora*, *Cyanea*, *Nemopilema*, and *Pelagia*), and cubozoans (*e.g*., *Carybdea*, and *Chironex*) in China, Japan, and Korea (Purcell *et al*., 2007; Dong *et al*., 2010). One of the most adverse events occurred in Haeundae Beach, the most popular swimming beach in Korea, in the summer of 2012, when a about 1,300 stinging incidents, primarily by *Chrysaora* and *Carybdea*, were reported. Due to global warming, subtropical venomous cubozoans such as *Chironex* are expanding their geographical ranges poleward, which could exert a new threat to coastal tourism in East Asia.

7 Ways to Reduce the Negative Impacts of Jellyfish

Shin-ichi Uye

Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Japan

7.1 Monitoring, prediction and forecast

Jellyfish may represent sentinels or indicators of environmental and ecosystem changes of coastal waters, as they often show trends in their abundance in relation to global warming, regional regime shifts, and various human impacts such as eutrophication, overfishing, and marine construction (Lynam *et al*., 2004; Purcell *et al*., 2007; Brodeur *et al*., 2008; Uye, 2011; Brotz *et al*., 2012; Condon *et al*., 2013). Hence, it is critical to emphasize the importance of monitoring jellyfish populations in regular surveys (Brodeur *et al*., 2016). However, attributes possessed by jellyfish, such as body fragility, patchy distribution, clear seasonality, and large yearly variation preclude robust assessment of their spatio-temporal distributions and abundance so that various sampling methods should be employed (see section 3).

For assessment of yearly variations in relative abundance of jellyfish populations, it is necessary to establish routine monitoring programs which should be conducted for prolonged periods over extended geographical ranges. The results from such jellyfish monitoring carried out by each PICES member country have been described in section 4. Among these, the monitoring programs conducted in the East Asian Marginal Seas by Korean and Japanese researchers are detailed in this section because they are designed to forecast the geographical transportation and magnitude of jellyfish blooms prior to the peak bloom season. If the blooms can be forecasted, it may be possible to alleviate their substantial negative impacts by taking proper countermeasures in advance.

7.1.1 Korean monitoring programs

As already described in section 4.9, the National Institute of Fisheries Science (NIFS) is currently conducting two routine jellyfish monitoring programs: the Korean Jellyfish Monitoring Network (KoJEM), primarily covering coastal waters, and the Korean Series of Oceanographic Monitoring Program (KSO) covering mostly the Korean exclusive economic zone (EEZ) in the Yellow Sea and the East China Sea, in addition to occasional aerial surveys using an aircraft. The KSO survey aims to detect an early sign of a potential bloom of *Nemopilema nomurai* in offshore waters near the border between Korea and China in June. If young medusae of *N. nomurai* occur at prominently higher densities over a notably wider area than usual in this area, they would be transported by currents to Korean coastal waters in a month or two, when they grow to approximately 1-m bell diameter, causing damage to coastal fisheries.

In the KoJEM survey, NIFS collects information on the presence/absence of jellyfish in various locations, aggregated or solitary occurrence, and approximate bell diameter of all jellyfish species, from a total of 294 appointed monitoring stations scattered nationwide at weekly intervals beginning in May (see Fig. 4.9.2). The collated data are uploaded to NIFS's homepage, from which the geographical location of the major jellyfish species can be updated weekly so that the arrival of *N. nomurai* in Korean coastal waters can be confirmed. Based on these monitoring programs, NIFS is able to give an early warning of a possible *N. nomurai* bloom in June or July, prior to the peak bloom season, *i.e.*, August and September, in Korean coastal waters.

7.1.2 Japanese monitoring programs

Sighting surveys using ships of opportunity

Although the benthic polyps of *N. nomurai* have not been found yet, they are likely distributed in the coastal waters along the large bay system flanked by the Korean Peninsula and the mainland of China, of which the Changjiang River estuary may constitute one of the main polyp habitats (see sections 4.8, 4.9 and 4.10). Being released as planktonic ephyrae from strobilated polyps in spring, young *N. nomurai* medusae are transported offshore with the local coastal current, and disperse over the entire Yellow Sea and the northern East China Sea in early summer. Then, this dispersed population is transported to the Tsushima Strait between Japan and Korea, and farther into Japanese waters, primarily by means of the northerly-flowing Tsushima Current. Hence, for the forecast of possible blooms in Japanese coastal waters, or the destinations of the expatriated medusa population, it is essential to monitor population abundance of young *N. nomurai* near the seeding and nursery grounds in early summer.

Japanese monitoring programs started in 2006 using ships of opportunity, sponsored by the Fisheries Research Agency, after serious damage to fisheries by consecutive *N. nomura* blooms from 2002 to 2005. There are two programs: one is conducted by Hiroshima University using international ferry routes between Japan (Shimonoseki and Osaka) and China (Qingdao, Shanghai, and Tianjin) covering the Yellow and northern East China Seas, and the other by the Japan Sea National Fisheries Research Institute using a ferry between Japan (Hakata) and Korea (Busan) covering the Tsushima Strait (Fig. 7.1.1). The monitoring is carried out from the ship deck during daytime by visual counting of medusae near the surface in a 10- or 15-m wide lane next to the ship's side for 5-min intervals, and the ship's geographical position is determined by a GPS at 15-min intervals. Since young medusae have never been sighted until May, when they grow large enough (bell diameter $\geq$ 10 cm) to be recognized from a 20-m-high deck of the ferry cruising at approximately 40 km h^{-1}, the monitoring is carried out once or twice a month during the period between June and November.

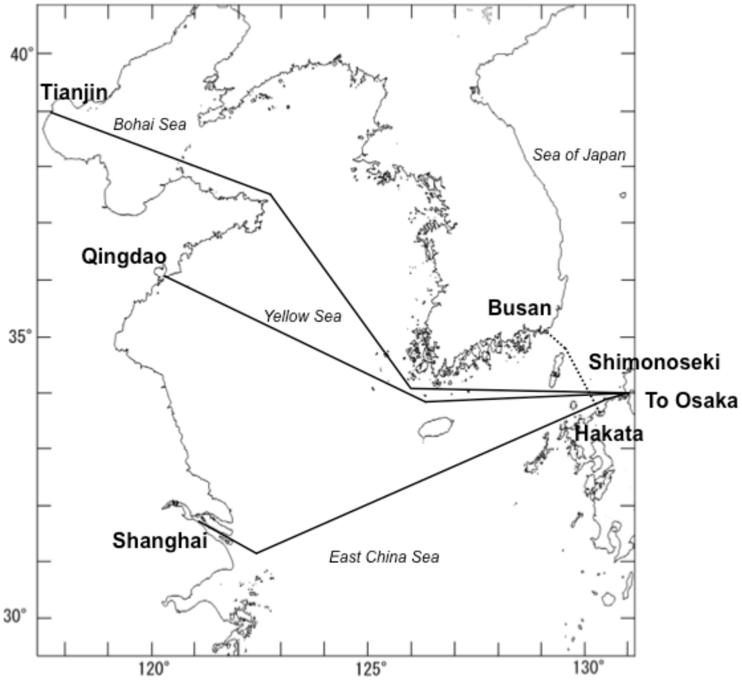


Fig. 7.1.1 International ferry routes used for monitoring *Nemopilema nomurai* by Japanese survey teams. Solid lines indicate the 3 routes between Japan (Shimonoseki and Osaka) and China (Tiangjin, Qingdao, and Shanghai). Dotted line shows the route between Japan (Hakata) and Korea (Busan).

In 2009, a prominent bloom year, young medusae were sighted for the first time in early June only in a relatively small area off the Changjiang River estuary. In late June, they were distributed in an extended area over the northern East China Sea and the central Yellow Sea at relatively high densites (average and maximum of 0.71 and 21 medusae 100 m^{-2}, respectively). Immediately after this ferry survey, an early warning of the bloom was announced nationwide through an information transfer system from Hiroshima University, through the Fisheries Research Agency, to the Japan Fisheries Information Service Center so local fishermen and fisheries cooperatives could be made aware of the possible appearance of these massive jellyfish in their fishing grounds. In early July 2009, *N. nomurai* occurred over the entire Bohai, Yellow and northern East China seas, and the highly aggregated frontal population (33 medusae 100 m^{-2}) started to clog fishing nets at Tsushima Island, located in the middle of the Tsushima Strait (Fig. 7.1.2). Medusa density reached a peak in early July, and then declined as the medusa were transported north through the Tsushima Strait, which was monitored by ferry between Hakata and Busan. Although there were extremely large annual differences in total population abundance (see Fig. 7.1.3 for 2014, a non-bloom year), the seasonal pattern in average density was basically similar each year, showing an annual peak in July.

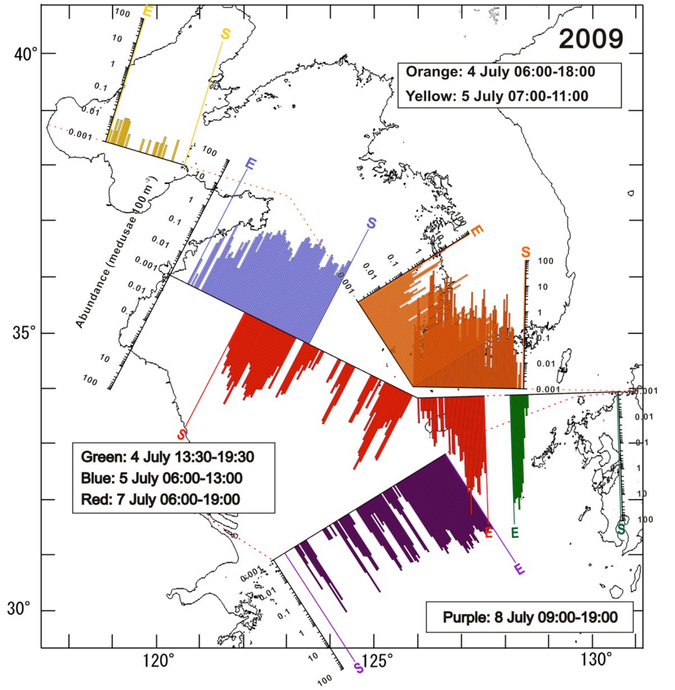


Fig. 7.1.2 Occurrence of *Nemopilema nomurai* in the Bohai Sea, Yellow Sea, and East China Sea along three cruise lines of ferries between Japan and China during July 4–8, 2009. S and E denote start and end points of daily sighting surveys. Each column represents the number of medusae counted in each 5-min interval (from Uye, 2010).

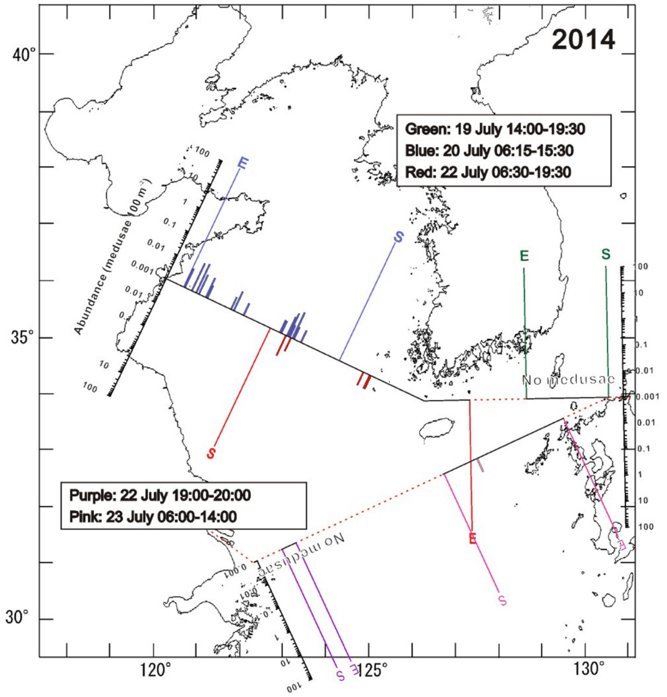


Fig. 7.1.3 Occurrence of *Nemopilema nomurai* in the Yellow Sea and East China Sea along two ferry routes between Japan and China from July 19–23, 2014. S and E denote start and end points of daily sighting surveys. Each column represents the number of medusae counted in each 5-min interval (from Uye *et al*., unpubl.).

Ten years of monitoring by ferry, conducted from 2006 to 2015, revealed that the average medusa density in the Yellow Sea in July had remarkable year-to-year variations (Fig. 7.1.4). In 2006, 2007, and 2009, densities were ≥2 medusae 100 m^{-2}, and Japanese coastal fisheries were devastated by a massive occurrence of *N. nomurai*, whereas in 2008, 2010, and 2011, when the densities were ≤0.05 medusae 100 m^{-2}, there were no damages to Japanese fisheries. In 2012, 2013, and 2015, when the densities were intermediate, modest damages occurred. Hence, on-deck sighting surveys from ferries can provide data to allow the forecasting of bloom intensity of *N. nomurai* in June or July of each year, 1 to 3 months prior to the massive occurrence of medusae in Japanese coastal waters.

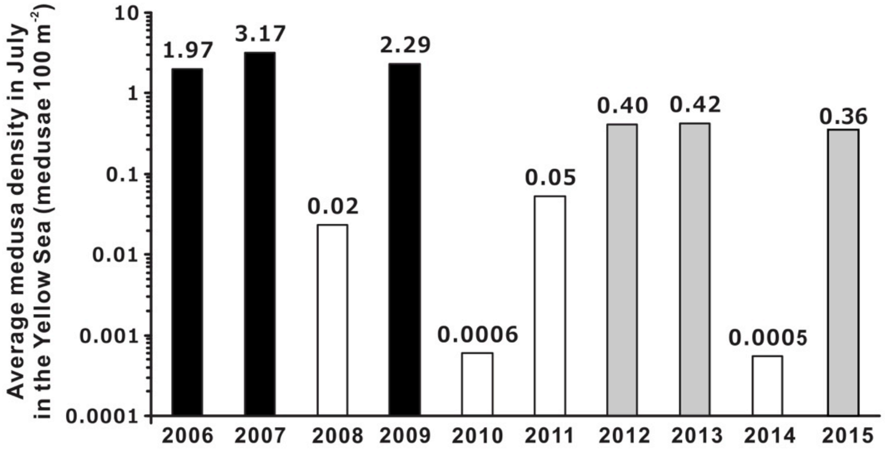


Fig. 7.1.4 Annual changes in average density of *Nemopilema nomurai* in the Yellow Sea in July, by ferry monitoring survey. Black, grey, and white columns indicate densities in prominent-, intermediate- and non-bloom years, respectively (from Uye *et al*., unpubl.)

Simulation model of jellyfish transport

After passage through the Tsushima Strait, the transport of *N. nomurai* medusae is subject to the flow of the Tsushima Current in the sea enclosed by the Asian continent and Japan, and hence a particle-tracking simulation model can forecast the horizontal trajectory of medusae on given dates. A simulation was performed by application of a forecast and hindcast system for the physical environment in the enclosed sea (Japan Sea Data Assimilation Experiment, JADE), developed by Japan Sea National Fisheries Research Institute, for particles mimicking medusae released in inshore, intermediate and offshore areas across the Tsushima Current during June 25 and July 7, 2009. In the simulation, the diel vertical migration behavior of the medusae, which occupy the shallow (8.8 m) layer during daytime for 15 hours and the deep (42.5 m) layer during nighttime for 9 hours (Honda *et al*., 2009), was also incorporated. Simulation results indicated that the frontal population would arrive near Noto Peninsula, jutting from the middle of Honshu, around August 10, and near Hokkaido around September 1 (Fig. 7.1.5). Since simulation results are accessible at the Japan Sea National Fisheries Research Institute's homepage (http://jsnfri.fra.affrc.go.jp/Kurage/kurage_top.html), local fishermen can obtain the information about the possible arrival time of medusae in their fishing grounds. This simulation also demonstrated that *N. nomurai* were distributed extensively offshore from the coast of Japan (Fig. 7.1.5).

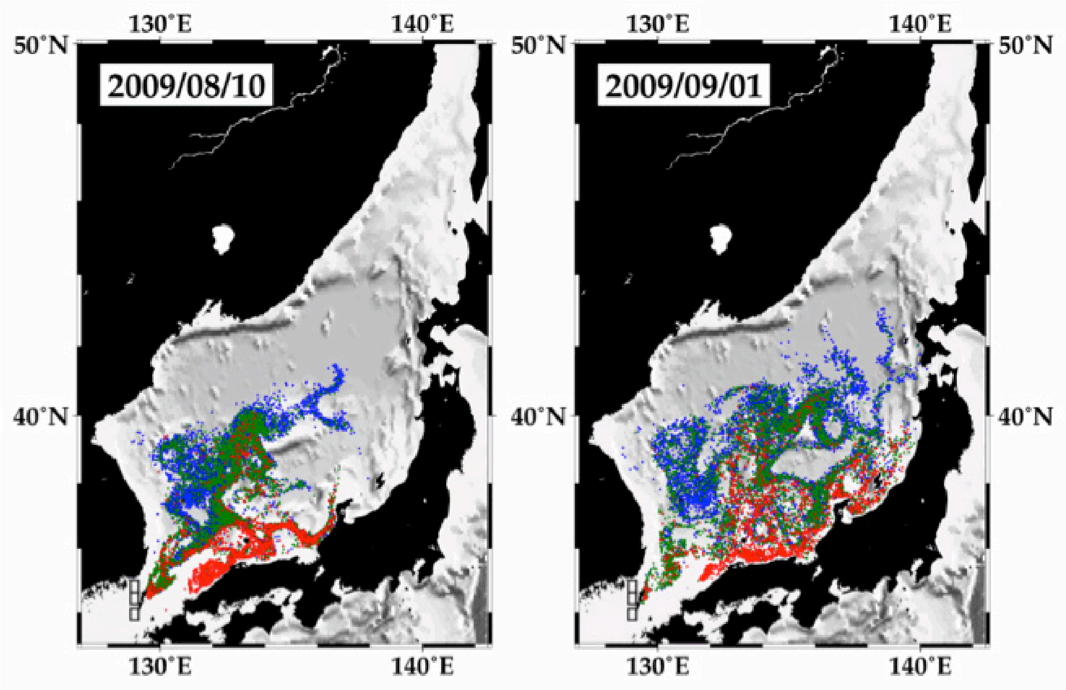


Fig. 7.1.5 Horizontal trajectory of *Nemopilema nomurai* medusae in the sea enclosed by the Asian continent and Japan on August 10 and September 1, 2009 predicted by a simulation model. Red, green, and blue particles mimic medusae released from the inshore, intermediate and offshore area (designated as each box), respectively, across the Tsushima Current during June 25 and July 7, 2009 (T. Watanabe and A. Okuno, unpubl.).

7.2 *Countermeasures*

7.2.1 Control of polyp populations

The life cycle of cnidarians alternates between a sexual planktonic medusa phase and an asexual benthic polyp phase. In the latter phase, the polyps can multiply asexually by various means such as budding, fission, podocyst formation, and strobilation to generate large populations (Arai, 1997; Lucas *et al.*, 2012), particularly on the underside of artificial structures (Willcox *et al.*, 2008; Purcell *et al.*, 2009; Toyokawa *et al.*, 2011; Duarte *et al.*, 2012; Makabe *et al.*, 2014). In *Aurelia aurita* s.l., for example, one polyp with an excess food supply and at 26°C can increase to 57 polyps in only 3 weeks, and one strobilating polyp can form as many as 21 discs (Ishii and Watanabe, 2003; Uye *et al.*, unpubl.), each of which transforms into a larval medusa (or an ephyra). These numbers suggest that a single polyp present in summer–fall in temperate coastal waters can potentially give birth to more than 1,000 ephyrae in winter, the season of ephyra release. Therefore, the asexual reproduction by polyps strongly determines the medusa population size in the following season. Hence, one of the most efficient countermeasures against medusa population outbreaks is to reduce the polyp population size in the field.

Physical removal

In Korea, the Polyp Countermeasure Program (PCP), which consists of three sub-programs: 1) the search for poly hotspots along the Korean coast, 2) the elimination of natural polyps, and 3) the assessment of the effect of polyp elimination on later medusa occurrence, has been conducted since 2009. In Sihwa Lake, one of the *A. aurita* sp. 1 polyp hotspots (see Fig. 4.9.12), polyp colonies attached to submerged pillars of 22 power transmission towers (out of total 32 towers) were physically removed using a high-pressure water jet operated by divers in April, 2013. A follow-up survey conducted a month later (May, 2013) revealed that only 0.93 million polyps out of an initial total of 134 million polyps remained attached to the treated pillars, demonstrating that 99.3% of the initial polyp abundance was eliminated in the removal operation. The survey also showed that the ephyra density (0.22 ephyrae m^{-3}) was extremely low in 2013 compared to the density (14 ephyrae m^{-3}) in May, 2011, prior to the removal project (I. Hwang, Korea Marine Environmental Corporation, pers. comm.). In addition, monitoring data of *A. aurita* sp. 1 medusae in coastal waters adjacent to Sihwa Lake showed a prominent decrease in medusa abundance after the polyp elimination in 2013. The Korean PCP team plans to proceed with this type of physical removal in other *A. aurita* sp. 1 polyp hotspots in future years.

Chemical approaches

Settlement and metamorphosis of planktonic larvae of marine benthic invertebrates, including cnidarian planulae, are influenced by various factors in the water (temperature, salinity, dissolved oxygen concentration), on substrates (surface topology, natural/artificial objects, chemical conditions, coverage with bacterial film and sessile organisms), and in their own physiology (age, nutritional conditions) (Crips, 1974; Rodríguez *et al*., 1993; Lucas et *al*., 2012). Among these factors, chemical cues are particularly important (Fusetani, 2003). To prevent economic damage due to the settling of various fouling organisms on ships' hulls, cooling systems of power stations, aquaculture cages, and other submergible structures, organotin compounds, including tributyltin (TBT) and tributyltin oxide (TBTO) had been used in antifouling paints. However, after a global ban on the use of these compounds entered into force in 2008, alternative antifouling paints containing various booster biocides (Konstantinou and Albanis, 2004) are used currently. The median lethal doses of five commercially available antifoulants, *i.e*., copper pyrithione (CuPT), Irgarol 1051, Sea-Nine 211, triphenylborane pyridine (TPBP), and zinc pyrithione (ZnPT), were tested on *A. aurita* s.l. polyps (Ishii and Nogata, unpublished). As their 24hLD_{50} (0.3–10.0 µg ml^{-1}) was much lower than that for barnacle and mussel larvae, these synthetic antifoulants are considered effective in targetting planula larvae from settlement but do not prevent other beneficial larvae from settling. Yet, these compounds may also pose a threat to the aquatic environment (Thomas, 2001).

Environmentally friendly antifoulants need to be developed, particularly for aquaculture structures. To combat the problem of net-fouling at a salmon farm in Tasmania, the effect of non-toxic silicone coating was examined (Hodson *et al*., 2000). The coated netting resulted in significantly less fouling by organisms, including hydrozoans (to 24% by wet weight), compared to uncoated netting after 163 days immersion, and fouling organisms that did settle loosely adhered to the silicone coating so that they were easily removed by cleaning. Since some marine invertebrates have developed various defense systems against biofouling, including chemical defenses, marine natural products showing antifouling characteristics have been isolated from them (Pawlik, 1993; Qian *et al*., 2009), and these are thought to be environmentally friendly. Methanol- and chloroform-soluble extracts from 22 Japanese marine species (2 algae, 15 sponges, 7 cnidarians, 3 echinoderms, 3 molluscans, and 2 ascidians) showed an antifouling effect for *A. aurita* s.l. planulae (Ishii and Nogata, unpubl.). Among the extracts, several cyclic peptides isolated from a red alga *Digenea simplex* collected at Ishigaki Island, Okinawa, demonstrated promising antifouling results; the substrate (glass or polycarbonate) coated with approximately 5 µg of one of these isolated peptides (referred as Type-B) per cm^2 completely inhibited the settlement of planulae (Ishii and Nogata, unpubl.).

Studies on natural compounds as non-toxic antifoulants specifically effective for cnidarian planulae are still preliminary, and more studies are needed to understand the practical use of these compounds. One of the largest obstacles may be how to obtain a sufficient amount of these effective compounds from marine organisms, the harvestable biomass of which is generally limited. If the underside of artificial structures in coastal waters can be coated with these compounds, this may be a sufficient deterrent to polyp settlement and reproduction.

Biological approaches

Predation is one of factors affecting the population size of cnidarian polyps. Nudibranchs are the best-known polyp predators (Hernroth and Gröhdalh, 1985; Gröhdalh and Hernroth, 1987; Hoover *et al*., 2012), and some other gastropods, pycnogonids, amphipods, and decapods also eat polyps (Oakes and Haven, 1971; Takao *et al*., 2014). The predation rates by some of these small benthic invertebrates are surprisingly high: up to 2,400 polyps day^{-1} by the nudibranch *Hermissenda crassicornis*, ~300 polyps day^{-1} by the trochid gastropod *Calliostoma unicum*, ~400 polyps day^{-1} by the shrimp *Rhynchocinetes uritai*, and ~700 polyps day^{-1} by the crab *Hyastenus diacanthus* (Hoover *et al*., 2012; Takao *et al*., 2014). In addition, frequent SCUBA dives conducted in Hiroshima Bay, Inland Sea of Japan, revealed that there were no occurences of *A. aurita* s.l. polyps in natural rock- and pebble-bedded areas, where numerous polyp predators inhabited compared to numerous *A. aurita* s.l. polyps found in fishing ports, particularly on the underside of floating piers where no or very few predators occurred (Takao *et al*., 2014). These facts imply that the interaction between jellyfish polyps and their natural enemies may be intense in the field, leaving *A. aurita* s.l. polyps to form large colonies only on substrates such as the underside of artificial structures, where natural predators are absent or very few.

Transplants of natural enemies with high predation capacity to polyp-aggregated substrates may be an effective method to eliminate polyps. For this purpose, the trochid gastropod *C. unicum* may be the best candidate because it is common in East Asian coastal waters and can adhere to overhanging structures. An experiment using transplanted *C. unicum* was conducted in a small fishing port in Hiroshima Bay, where there was a floating pier (length: 48 m, width: 6 m, average polyp density: 30,000 polyps m^{-2}), and it was found that a single *C. unicum* could eat approximately 40 polyps per hour (Takao *et al*., 2014). Assuming that the predation rate of a *C. unicum* is 300 polyps day^{-1}, and that there is no asexual reproduction of polyps, all the polyps on the pier (estimated to be ~9 million, Makabe *et al*., 2014) could be eliminated within a month or so, if a density of 3 *C. unicum* per m^2 were transplanted there. The best time for killing polyps by transplanted predators would be in the autumn, just before the initiation of strobilation, which regularly starts in December in the Inland Sea of Japan. An assessment of negative ecological impacts, if any, created by transplanted predators is needed before this biological control of *A. aurita* s.l. can be put into practice.

7.2.2 Medusa slicing

One of the countermeasures used by Japanese fishermen for combatting the abundance of medusae is to slice them with so-called jellyfish cutters using carbon steel wires at the cod-end of trawls. This method of killing *N. nomurai* was attempted for the first time during the summer of 2005 when a massive bloom of this species devastated Japanese coastal fisheries. However, it was ineffective in reducing jellyfish damage because the operation was confined to small areas compared to the vast geographical range of *N. nomurai* distribution. Therefore, slicing may only be useful for highly aggregated jellyfish patches in local areas.

Slicing was also employed to kill *A. aurita* s.l. in the eastern Inland Sea of Japan by a group of boat seiners of the Boze Fisheries Cooperative in Himeji. The boat seine fisheries have been suffering from massive occurrences of *A. aurita* s.l. since the 1990s, and were most severely affected in the early 2000s (Uye and Ueta, 2004). Fishermen found that prior to the fishing season for larval anchovy (summer and autumn), *A. aurita* s.l. regularly formed dense aggregations in relatively confined coastal areas. To slice them before being dispersed to their fishing grounds, the fishermen invented a jellyfish cutting net (length: 7 m, width: 3.5 m) towed by a pair of boats, and then performed an intensive slicing operation using 30 pairs of boats for 17 days (for 5 hours per day) between April 20 and May 16, 2010. Through this operation, an estimated 1×10^8 medusae (equivalent wet weight biomass: approximately 3×10^4 tons) were removed, which resulted in a higher catch of larval anchovy compared to previous years. The project continued for 3 years with financial support from the government, but stopped thereafter due to arguments between fishermen and government about cost and benefit of the slicing.

7.2.3 Fishing net structural modifications

All net-based fisheries are more or less damaged by entrapped jellyfish, and various types of jellyfish-excluding devices have been invented and deployed (Graham *et al*., 2014; Lucas *et al*., 2014). JET (Jellyfish Excluder for Towed fishing gear), a device similar to the TED (Turtle Excluder Device) used in shrimp trawls (Watson *et al*., 1993, Mitchell *et al*., 1995), was designed to remove *A. aurita* s.l. and *N. nomurai* from towed fishing nets (Fig. 7.2.1, Matsushita and Honda, 2006), and has been successfully used by Japanese fishermen during bloom years (Matsushita *et al*., 2005; Okino *et al*., 2009).

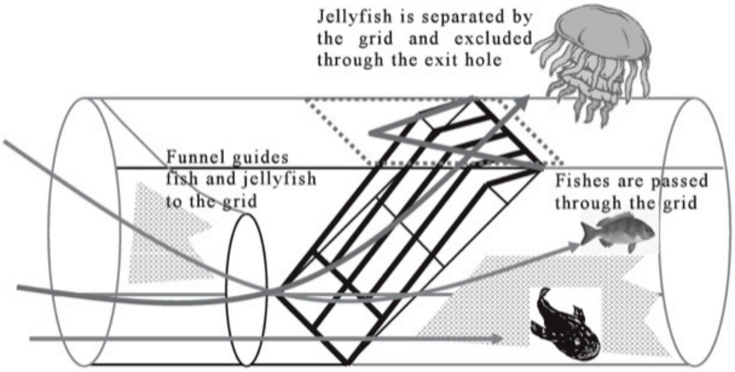


Fig. 7.2.1 Schematic showing the separation of jellyfish from target fish species by JET (from Matsushita and Honda, 2006).

There are approximately 2,000 set nets, the scale of which varies from small ones handled by 2 or 3 people to large ones operated by 20 to 30 fishermen, along the coast of Japan affected by *N. nomurai* blooms, and the damage is always greatest in the set net fisheries. To alleviate the damage, traditional set nets have been modified by: 1) mesh size enlargement of the leading nets in order to prevent medusae from blocking the net, 2) installation of bypass nets to route approaching medusae outside the net, and 3) installation of a partition net to separate medusae from fish and remove them outside the net (Fig. 7.2.2). Although it cost 5–10 million JPY (~45,000–90,000 USD) to introduce such modifications for a large set net, the benefits outweighed the initial cost as the modified set nets functioned effectively to remove entrapped medusae (subsequently usually less than a hundred medusae were trapped per net per day) and yielded regular fish catches even during the months of heaviest aggregation (October–December) in 2009. On the other hand, set nets that were not modified were so severely damaged by more than several thousand entrapped medusae that operations had to be halted during the regular fishing season during that year.

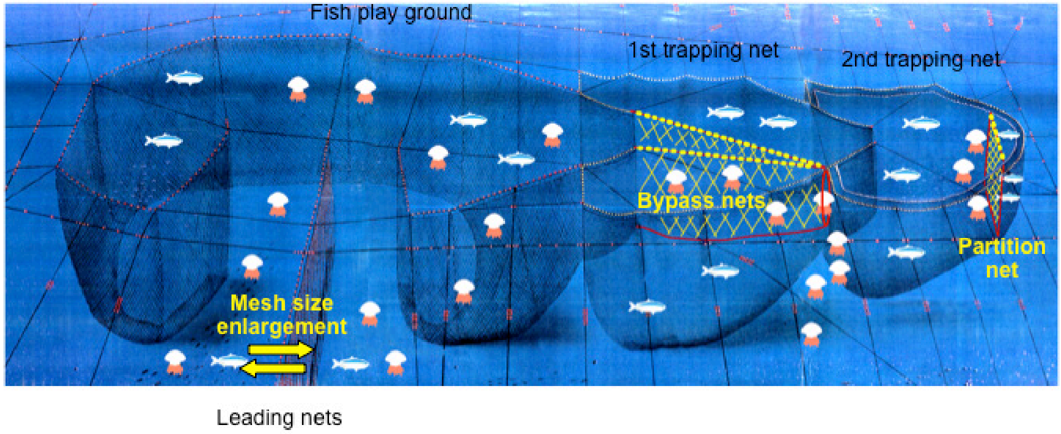


Fig. 7.2.2 Schematic representation of a traditional set net modified to exclude *Nemopilema nomurai* medusae by: 1) mesh size enlargement of the leading nets, 2) installation of bypass nets, and 3) installation of a partition net (figure courtesy of R. Matsuhira).

8 Conclusions and Prioritized Recommendations for Future Research

Richard Brodeur[1] and Shin-ichi Uye[2]

[1] Northwest Fisheries Science Center, Hatfield Marine Science Center, National Marine Fisheries Service, NOAA, Newport, Oregon, USA
[2] Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Japan

Based on the information presented in this report, much progress has been made in the PICES region in terms of examining the distributions and trends in abundance of the dominant gelatinous zooplankton in the North Pacific and its marginal seas. Clearly, some areas have had more work done than others, but a substantial body of knowledge exists for the PICES region compared to other areas of the world's ocean. Much is also known about the biology and ecology of the dominant gelatinous species, but more needs to be done to determine how increasing abundances of these taxa, seen in many ecosystems, may affect the marine resources that PICES member countries and other nations depend on. As a way of stimulating future lines of research, we propose the following recommendations:

1. Determine the physical or biological factors, both natural and anthropogenic, that may lead to jellyfish blooms in coastal waters;
2. Assess the potential for predicting the occurrence and magnitude of blooms from ½ to 2 years in advance to provide early warning for coastal ecosystems and the ecosystem services (fishing, aquaculture, tourism) that depend on them;
3. Establish early-warning monitoring systems on early life stages of jellyfish in areas prone to jellyfish blooms so that stakeholders can be notified of upcoming bloom events with sufficient time to take countermeasures for their impact. Incorporate larval distributions into detailed physical models of the ecosystem to predict where outbreaks will occur;
4. Provide quantitative estimates of the impact large blooms have on fisheries and other ecosystem components through field and laboratory studies and advanced ecosystem models to estimate trophic (competition, predation) interactions with key components of the ecosystem;
5. Work with the fishing industry to develop techniques to minimize the bycatch of jellyfish in commercial fisheries, whether through alterations of fishing locations/times or through modifications of gear to exclude jellyfish catches;
6. Work with benthic or nearshore ecologists to control the development of the polyp stages in large scyphozoans so that the size of the blooms are diminished. This could entail introducing predators on the polyp stage (biocontrol) or physical and chemical (biocides) manipulation of the attachment sites or substrate;

7. Study jellyfish blooms from biogeochemical viewpoints, particularly their roles in the enhancement of microbial food webs and carbon sequestration;
8. Promote more international collaboration, including multinational projects and cruises, to bring together expertise from a number of countries to work on mutual problems such as developing more efficient sampling gears or ecosystem monitoring programs.

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Section 2

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Section 5

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Appendix 1

WG 26 Terms of Reference

1. Review past and ongoing studies on the reproductive biology of jellyfish species that cause problematic blooms;
2. Compile existing data on temporal variations in jellyfish abundance in the North Pacific and its marginal seas, and analyze them in relation to regional environmental and climate changes in order to identify causes of increasingly recurrent jellyfish blooms;
3. Elucidate the role of jellyfish in coastal and oceanic marine food webs and assess the impacts of jellyfish blooms on marine ecosystems and socio-economies such as fisheries and aquaculture;
4. Evaluate methodologies for predicting blooms and for diminishing their impact on marine and human systems, including bloom forecast modeling and the modification of fishing gears;
5. Promote international collaboration among PICES member countries for exchanging available information on jellyfish, and encourage joint research surveys on jellyfish among PICES member countries;
6. Provide jellyfish metrics as an indicator of ecosystem change and resiliency in cooperation with FUTURE AICE-AP and SOFE-AP and FUTURE related expert groups;
7. Publish a final report summarizing the results, including recommendations to policy makers for reducing impacts of jellyfish blooms in the North Pacific.

Appendix 2

WG 26 Membership

Canada

Mary Needler Arai
Fisheries and Oceans Canada
Pacific Biological Station
3190 Hammond Bay Rd.
Nanaimo, BC, V9T 6N7
Canada
E-mail: araim@shaw.ca

Lucas Brotz
Fisheries Centre, Sea Around Us Project
University of British Columbia
2202 Main Mall
Vancouver, BC, V6T 1Z4
Canada
E-mail: l.brotz@fisheries.ubc.ca

Moira Donald Galbraith
Fisheries and Oceans Canada
Institute of Ocean Sciences
P.O. Box 6000
Sidney, BC, V8L 4B2
Canada
E-mail: Moira.Galbraith@dfo-mpo.gc.ca

Japan

Hideki Akiyama (2010–2012)
East China Sea Fisheries Oceanography Division
Seikai National Fisheries Research Institute
FRA
1551-8 Taira-machi
Nagasaki 851-2213
Japan
E-mail: hakiyama@fra.affrc.go.jp

Haruto Ishii
Tokyo University of Marine Science
4-5-7 Minato, Tokyo 108-8477
Japan
E-mail: ishii@kaiyodai.ac.jp

Masaya Toyokawa (2012–2013)
Seikai National Fisheries Research Institute
FRA
1551-8 Taira-machi
Nagasaki 851-2213
Japan
E-mail: mtoyokaw@affrc.go.jp

Shin-ichi Uye (WG 26 Co-Chair)
Graduate School of Biosphere Science
Hiroshima University
4-4 Kagamiyama 1 Chome
Higashi-Hiroshima, Hiroshima 739-8528
Japan
E-mail: suye@hiroshima-u.ac.jp

People's Republic of China

Siqing Chen
Yellow Sea Fisheries Research Institute
CAFS
106 Nanjing Rd.
Qingdao, Shandong 266071
People's Republic of China
E-mail: chensq@ysfri.ac.cn

Xinming Pu
Marine Ecology Research Center
First Institute of Oceanography, SOA
Qingdao, Shandong 266061
People's Republic of China
E-mail: xmpu@fio.org.cn

Song Sun
Institute of Oceanology, CAS
7 Nanhai Rd.
Qingdao, Shandong 266071
People's Republic of China
E-mail: sunsong@ms.qdio.ac.cn

Zijun Xu
North China Sea Branch of SOA
22 Fushun Rd.
Qingdao, Shandong 266000
People's Republic of China
E-mail: zjxu77@gmail.com

Republic of Korea

Changhoon Han
National Institute of Fisheries Science
(formerly National Fisheries Research and
Development Institute), MOF
152-1 Haean-ro, Gijang-eup, Gijang-gun
Busan 619-705
Republic of Korea
E-mail: chhan@korea.kr

Young-Shil Kang (WG 26 Co-Chair,
Oct. 2010–Oct. 2011)
National Fisheries Research and Development
Institute, MIFAFF
408-1 Shirang-ri, Kijang-up, Kijang-gun
Busan 619-705
Republic of Korea
E-mail: yskang@nfrdi.go.kr

Kyoungsoon Shin
Korea Institute of Ocean Science and Technology
(KIOST)
41 Jangmok1-gil Jangmok-Myon
Geoje 656-834
Republic of Korea
E-mail: ksshin@kiost.ac

Won-Duk Yoon (2010–2012;
WG 26 Co-Chair, Oct. 2011–Dec. 2012)
National Fisheries Research and Development
Institute, MIFAFF
408-1 Shirang-ri, Kijang-up, Kijang-gun
Busan 619-705
Republic of Korea
E-mail: wdyoon@nfrdi.go.kr

Seungshic Yum (2013)
South Sea Environment Research
Korea Institute of Ocean Science and Technology
(KIOST)
Geoje, Gyeongnam 656-830
Republic of Korea
E-mail: syum@kiost.ac

Russian Federation

Elena P. Dulepova
Pacific Scientific and Research Fisheries Center
(TINRO-Center)
4 Shevchenko Alley
Vladivostok 690091
Russia
E-mail: dep@tinro.ru

Alexander V. Zavolokin
Pacific Scientific and Research Fisheries Center
(TINRO-Center)
4 Shevchenko Alley
Vladivostok 690950
Russia
E-mail: aleksandr.zavolokin@tinro-center.ru

United States of America

Richard D. Brodeur (WG 26 Co-Chair)
Northwest Fisheries Science Center
NMFS, NOAA
2030 SE Marine Science Dr.
Newport, OR 97365
USA
E-mail: Rick.Brodeur@noaa.gov

Kristin Cieciel
Auke Bay Laboratories
Alaska Fisheries Science Center, NMFS, NOAA
17109 Pt. Lena Loop Rd.
Juneau, AK 99801
USA
E-mail: kristin.cieciel@noaa.gov

John C. Field
Southwest Fisheries Science Center
NMFS, NOAA
110 Shaffer Rd.
Santa Cruz, CA 95060
USA
E-mail: John.Field@noaa.gov

Jennifer E. Purcell
Shannon Point Marine Center
Western Washington University
1900 Shannon Point Rd.
Anacortes, WA 98221
USA
E-mail: purcelj3@wwu.edu

Appendix 3

Meeting Reports and Topic Session/Workshop Summaries from Past Annual Meetings Related to WG 26

PICES

ICES

PICES Fifteenth Annual Meeting (PICES XV)

October 13–22, 2006
Yokohama, Japan

Extracted from:

2006 Summary of Scientific Sessions and Workshops at PICES XV

BIO/FIS Topic Session (S2)
The human dimension of jellyfish blooms

Co-convenors: Richard Brodeur (U.S.A.), Jiahua Cheng (China), Horoshi Iizumi (Japan) and Won Duk Yoon (Korea)

Background

Large, high-density jellyfish blooms are becoming increasingly common in many marginal seas in the North Pacific and in other regions of the world's oceans, and may be important regulators of marine ecosystems. These blooms may have direct effects on fish recruitment through predation on vulnerable early life stages of marine fishes, or indirect effects competing for limited food resources with exploited species. In addition, high concentrations of jellyfish influence humans in other ways like economic losses in tourism through beach closures, impeding commercial fishing through net clogging, and loss of energy production through clogging of power plant intakes. If jellyfish populations continue to increase in the coming decades, their impacts on human populations are also likely to increase. This session sought to understand the causes of the proliferation and expansion of these blooms in coastal waters and whether climatic or anthropogenic changes have led to the recent blooms. In this regard, studies that examined the effects of these blooms on humans and their economies, and ways to predict their occurrence and spread were encouraged.

Summary of presentations

The session consisted of 13 oral and 7 poster presentations. The invited talks focused on factors that have led to increases in gelatinous zooplankton in a number of regions around the world. Jellyfish have replaced some major fish resources and have caused substantial damage to human endeavors such as fishing, aquaculture, the generation of electricity, and tourism. The economic implications of these blooms can be staggering, leading to complete loss of some very valuable fisheries. One of the more important ideas brought out at the session was the concept of a 'jellyfish spiral' where many factors acting synergistically cause jellyfish to increase, and once these jellyfish populations are established, reverting to fish dominated ecosystems is difficult. However, in several case studies, including the Bering Sea and Black Sea, there can be decreases in jellyfish populations due to decreased production and by the introduction of jellyfish predators, respectively.

Many of the contributed papers discussed case studies in different regions of the world, with a substantial emphasis on the giant jellyfish that has been appearing in East Asian waters in the last decade. Three contributed talks and one poster covered North American studies in the Bering Sea, California Current and Northwest Atlantic. The subjects of talks covered not only the pelagic adult stage that is most visible but also the benthic polyp stage, about which we know relatively little for many species. Several presentations discussed ways of estimating jellyfish abundance by acoustics, examining the stomachs of predators, and by aerial photography. Numerical models of ocean circulation were shown to be an effective means of examining jellyfish dispersal in coastal waters. Several studies have started to use ecosystem models to assess the effects of jellyfish on ecosystems, and some success has been achieved.

It became apparent during the session that jellyfish have been increasing in a number of ecosystems around the world and that with current scenarios of ocean change due to warming, overfishing, eutrophication, and habitat modification, we can expect to see this trend continue in the future. The fishing industry is beginning to adapt to these changes by employing jellyfish excluders on trawl nets and by finding new markets for jellyfish products. Some of the participants of the session met separately with representatives of the power generation industry to provide advice on ways to predict or control jellyfish ingress in power plant cooling systems. Cooperation between scientists and industry will be essential in adverting what could become both an ecological and financial crisis in the future.

The convenors planned to produce a special issue of the journal, *Plankton and Benthos Research*, containing peer-reviewed papers from the session.

List of papers

Oral presentations

Jennifer E. Purcell (Invited)
Interactions of multiple factors contribute to infestations of jellyfish

Shin-ichi Uye (Invited)
Bloom of the giant jellyfish *Nemopilema nomurai*: A threat to the East Asian Marginal Seas fisheries sustainability

Tamara A. Shiganova (Invited)
Comparative analyses of invasive gelatinous species blooms in the Black, Azov, Caspian and Aegean Seas and their effect on ecosystems and fisheries

Hitoshi Iizumi, Osamu Katoh, Tatsuro Watanabe, Naoki Iguchi, Koh Nishiuchi, Toru Hasegawa, Kosei Komatsu, Kazufumi Takayanagi and Masaya Toyokawa
Mass appearance of the giant jellyfish, *Nemopilema nomurai*, along the coastal area of Japan

Joon-Yong Yang, Soo-Jung Chang, Jae Hong Moon, Won Duk Yoon and Donghyun Lim
Distribution of *Nemopilema nomurai* in Korean waters in 2005 and its possible origin

Jia-Hua Cheng, Feng-Yuan Ding, Sheng-Fa Li and Hui-Yu Li
Study on the quantitative distribution pattern of macro-jellyfish in the East China Sea

Jason S. Link, Michael D. Ford and Elizabeth Fulton
Widespread and persistent increase of Ctenophora in the Northeast U.S. shelf ecosystem: Evidence from spiny dogfish (*Squalus acanthias*) and implications for large marine ecosystems

Hye Eun Lee, Won Duk Yoon and Donghyun Lim
Predator on polyps of *Nemopilema nomurai* (Scyphzoa, Rhizostomeae)

Kristin Cieciel, Lisa Eisner, Angela Feldmann and Mary Courtney
Size structure, distribution, and interaction characteristics of dominant jellyfish from surface trawls in the Eastern Bering Sea

Haruto Ishii
Adaptation to coastal environmental changes in the polyp stage in relation to jellyfish blooms in Tokyo Bay

Richard D. Brodeur, Cynthia Suchman, Doug Reese, Todd Miller, Jim Ruzicka and Elizabeth Daly
Spatial overlap and trophic interactions between fish and large jellyfish in the northern California Current

Jing Dong, Chun-Yang Liu, Yang-Qing Wang and Bin Wang
Laboratory observations on the life cycle of *Cyanea nozakii* (Semeostomida, Scyphozoa)

Miyuki Hirose, Tohru Mukai, Kohji Iida and Doojin Hwang
Acoustic observations on the jellyfish *Nemopilema nomurai* in the East China Sea

Posters

Naoki Fujii, Akiko Fukushima, Yuta Nanjo and Hidetaka Takeoka
Aggregations of *Aurelia aurita* in Uwa Sea, Japan

Hye Eun Lee, Won Duk Yoon and Donghyun Lim
The prey passage of *Nemopilema nomurai* (Scyphozoa, Rhizostomeae)

Seok Hyun Lee, Won Duk Yoon and Dong Hyun Lim
Effect of heavy metals on polyps of the *Aurelia aurita*

Xiancheng Qu, Masaya Toyokawa, Ying Liu and Yasuaki Nakamura
Molecular biological analysis of jellyfish (*Nemopilema nomurai kishinouye*) mitochondrial 18S ribosomal RNA

James J. Ruzicka, Thomas C. Wainwright and Richard D. Brodeur
Trophic interactions within the pelagic community of the Oregon and Washington upwelling ecosystem: A modeling study of the role of large jellyfish

Jun Shoji
Quantitative and qualitative changes in predator-prey relationship between moon jellyfish and fish larvae in summer hypoxia: Possible increase in trophic flow to jellyfish in coastal ecosystems

Euikyung Kim, Seunghwan Lee, Jong-Shu Kim, Won Duk Yoon, Donghyun Lim, Andrew J. Hart and Wayne C. Hodgson
Cardiovascular effects of *Nemopilema nomurai* (Scyphozoa, Rhizostomeae) jellyfish venom in rats

PICES Eighteenth Annual Meeting (PICES-2009)

October 23–November 1, 2009
Jeju, Korea

Extracted from:

Summary of Scientific Sessions and Workshops at PICES-2009

BIO Workshop (W2)

Standardizing methods for estimating jellyfish concentration and development of an international monitoring network

Co-Convenors: Hideki Akiyama (Japan), Richard Brodeur (U.S.A.) and Young-Shil Kang (Korea)

Background

Large high-density jellyfish blooms are becoming increasingly common in many marginal seas in the North Pacific and in other regions of the world's oceans, and may be important regulators of marine ecosystems. These blooms may have direct effects on fish recruitment through predation on vulnerable early life stages of marine fishes, or indirect effects competing for limited food resources with exploited species. In addition, high concentrations of jellyfish influence humans in other ways like economic losses in tourism through beach closures, impeding commercial fishing through net clogging, and loss of energy production through clogging of power plant intakes. If jellyfish populations continue to increase in the coming decades, their impacts on human populations are also likely to increase. However, our understanding of these blooms is hindered by a lack of standardization in sampling and insufficient monitoring. The goals of this workshop were to 1) understand the problems and develop techniques for estimating concentrations of jellyfish, 2) evaluate the status of national monitoring systems, 3) emphasize why standard methods and international monitoring are needed, and 4) develop an implementation plan and schedule for improving abundance and distribution information on jellyfish blooms.

Summary of presentations

The session consisted of 1 invited and 9 contributed oral presentations. The invited talk specifically focused on the advantages and deficiencies of the various methods that have been used to estimate the abundance of gelatinous zooplankton in a number of systems around the world. These included using by-catch in fishery surveys, acoustics, aerial surveys, underwater cameras, shore-based surveys, ships of opportunity, and predictive modeling. For non-quantitative patterns of spatial and temporal abundance, these large-scale methods can effectively be used to monitor jellyfish populations but each has its own bias. To measure ecological effects we also need to: 1) calibrate large-scale methods against quantitative methods, 2) determine numbers and biomass, and 3) estimate trophic importance. Also discussed was how physiological parameters such as respiration rates can be used to measure trophic impacts of jellyfish populations.

Many of the contributed papers discussed particular case studies in different regions of the world, with a substantial emphasis on the giant jellyfish that has been appearing in East Asian waters in the last decade. Two contributed talks discussed acoustic methods (echo counting) and compared these estimates from other methods. Another talk focused on using regularly scheduled ferries between Japan and China to estimate jellyfish abundance visible from the deck. Three talks used video surveys to examine vertical and spatial distribution of smaller medusae off Japan and the west coast of the U.S. in comparison to trawl or sighting surveys. The latter also included using models to predict habitat and interannual catches of jellyfish. One talk used a sonar (DIDSON) system to examine the finer-scale distribution of jellyfish and provided density estimates three times as high as net sampling. The last talk used numerical particle-tracking models to predict the arrival time of giant jellyfish to Japanese waters. Numerical circulation models were shown to be effective means of examining jellyfish dispersal in coastal waters but best results were obtained if vertical migration was incorporated into the modes. It became apparent that many novel techniques have been applied and some effort has gone into the efficacy of the different systems for estimating jellyfish abundance.

The final part of the workshop focused specifically on the jellyfish problem confronting the Asian east marginal seas with the yearly occurrence of the giant jellyfish blooms. The scale of the problem requires a substantial dedication of resources that may be beyond the ability of one laboratory or even one country to provide and it was broadly accepted that an international effort, coordinated by PICES, should be implemented. One way to accomplish this may be to assemble an international team of experts familiar with different sampling methods to participate on a PICES cruise to intercalibrate these methods to choose the best standard sampling to implement in all regions. Ship time would have to be contributed by the affected countries, but PICES could assist in coordinating research and help to disseminate results by sponsoring followup workshops. In the following years, cruises using multiple sampling gears and methods could be conducted in other jellyfish bloom 'hotspots'. The participants felt strongly that monitoring efforts in place now, including using ships of opportunity, should be continued and expanded where possible, and information on the magnitude and movement of on-going blooms should be expeditiously disseminated to all countries that may potentially be affected.

List of papers

Oral presentations

Jennifer E. Purcell (Invited)
Broad-scale research on jellyfish

Kazuhiro Sadayasu, Yoshimi Takao and Ryuichi Matsukura
Echo trace counting method for estimating the giant jellyfish *Nemopilema nomurai* density and distribution using a quantitative echosounder

Kyoung-Hoon Lee, Soo-Jeong Jang, Won Duk Yoon, Chang-Doo Park and Seong-Wook Park
Density estimates of *Nemopilema nomurai* jellyfish in Yellow Sea during 2006-2009

Hideki Ikeda, Hiroko Okawachi, Atsushi Yoshida, Miwa Hayashi and Shin-ichi Uye
Spatio-temporal distribution of the giant jellyfish *Nemopilema nomurai* in East Asian waters by sighting survey from a ferry

Haruto Ishii, Yasuyuki Nogata and Noriaki Endo
Horizontal and vertical distribution of jellyfish, *Aurelia aurita* medusae, and estimation of its abundance with underwater video system in Tokyo Bay

Richard D. Brodeur, Cynthia L. Suchman, Elizabeth A. Daly and Lanaya N. Fitzgerald
Habitat and ecology of large medusa in the northern California Current: An overview of recent studies

Naoki Fujii, Shinya Magome, Atsushi Kaneda and Hidetaka Takeoka
Monitoring method for moon jellyfish abundance in the western Seto Inland Sea, Japan

Hao-Hsien Chang, Chang-Yu Lai, and Wen-Tseng Lo
A study on the ecological significance of the box jellyfish, *Carybdea rastonii* Haacke (Cnidaria: Cubozoa), from the east coast of Taiwan

Chang-Hoon Han and Shin-ichi Uye
Quantification of the abundance and distribution of the common jellyfish *Aurelia aurita* s.l. with a Dual-frequency IDentification SONar (DIDSON)

Akira Okuno, Tatsuro Watanabe, Naoto Honda and Katsumi Takayama
Jellyfish transport simulation taking the diurnal vertical migration into account

PICES Twentieth Annual Meeting (PICES-2011)

October 14–23, 2011

Khabarovsk, Russia

Report of Working Group on *Jellyfish Blooms around the North Pacific Rim: Causes and Consequences*

The Working Group on *Jellyfish Blooms around the North Pacific Rim: Causes and Consequences* (WG 26) held its first meeting from 14:00 to 19:15 h on October 15, 2011 in Khabarovsk, Russia, under the local chairmanship of Prof. Shin-ichi Uye (Japan) and remote chairmanship of Dr. Richard Brodeur (USA). A total of 14 members and 5 observers participated in the meeting (*WG 26 Endnote 1*). The agenda for the meeting can be found in *WG 26 Endnote 2*.

AGENDA ITEM 2

Objectives and goals of WG 26

The Group confirmed the objectives and goals based on the Terms of Reference for WG 26.

Overview of jellyfish blooms and related research in members' countries

1. Canadian Pacific waters were reviewed by Lucas Brotz. He also provided an overview of the global picture of jellyfish blooms that he had studied for his recent Master's thesis.
2. Chinese waters were reviewed by Siqing Chen and Zijun Xu. Dr. Chen described the results of a national project on the Key Process, Mechanism and Ecological Consequences of Jellyfish Blooms in China Coastal Waters. Dr. Xu explained another national project, mainly focusing on the establishment of a monitoring system for early warning of possible jellyfish blooms.
3. Jellyfish in Japanese waters were reviewed by Hideki Akiyama and Shin-ichi Uye. Dr. Akiyama reported a China-Japan-Korea International Project on the Giant Jellyfish Bloom. Prof. Uye summarised the results of studies carried on under the Prediction and Control of Jellyfish Outbreak (STOPJELLY) Project.
4. Jellyfish in Korean waters were reviewed by Dr. Changhoon Han.
5. Jellyfish in Russian Pacific waters were reviewed by Dr. Alexander Zavolokin.
6. Jellyfish in U.S. Pacific waters were reviewed by Dr. Jennifer Purcell.

AGENDA ITEM 3

Draft outline for the Working Group report

Following a brief explanation by Prof. Uye on the tentative outline of the working group report, WG 26 discussed the viewpoint, target, structure, *etc.* of the report. The Co-Chairs will revise the tentative outline and email the members for further comments. Collaborative studies among PICES member countries were proposed to tackle some topics, such as sampling problems.

AGENDA ITEM 4
Proposal of a jellyfish blooms topic session at PICES-2012

Prof. Uye reported on a proposal for a topic session at PICES 2012 in Hiroshima that was submitted to the BIO Committee (*WG 26 Endnote 3*). The proposal is entitled "*Jellyfish in marine ecosystems and their interactions with fish and fisheries*". Because of the high importance and popularity of the topic, the Co-Chairs believe that it is likely to be approved. This 1-day topic session will be a good opportunity to show WG 26 activity to the PICES community.

AGENDA ITEM 5
Change of co-chair

The current Co-Chair from Korea, Dr. Young-Shil Kang, will be replaced with Dr. Won-Duk Yoon.

AGENDA ITEM 6
Closing

Prof. Uye expressed his thanks to all participants for their enthusiastic discussion and cooperation for making the first Working Group meeting successful.

WG 26 Endnote 1

WG 26 participation list

Members

Hideki Akiyama (Japan)
Richard Brodeur* (USA, Co-Chairman)
Lucas Brotz (Canada)
Siqing Chen (China)
Kristin Cieciel (USA)
Elena Dulepova (Russia)
John Field (USA)
Changhoon Han (Korea)
Haruto Ishii (Japan)
Xinming Pu (China)
Jennifer Purcell (USA)
Shin-ichi Uye (Japan, Co-Chairman)
Zijun Xu (China)
Alexander Zavolokin (Russia)

Observers

Sonia Batten (Canada)
David Checkley (USA)
Cynthia Suchman (USA)
YongJiu Xu (China)
Mingyuan Zhu (China)

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*via Skype

WG 26 Endnote 1

WG 26 meeting agenda

1. Opening remarks
2. Objectives and goals of WG 26
3. Draft outline for the Working Group report
4. Proposal of a jellyfish blooms topic session at PICES-2012
5. Change of co-chair
6. Closing

WG 26 Endnote 3

Proposal for a 1-day BIO/FIS Topic Session at PICES-2012 on "*Jellyfish in marine ecosystems and their interactions with fish and fisheries*"

Convenors: Shin-Ichi Uye (Japan), Richard Brodeur (USA), Song Sun (China), Won-Duk Yoon (Korea)

Evidence is accumulating that gelatinous zooplankton populations have increased substantially in many regions of the world, most likely through anthropogenic stresses, but we have insufficient understanding of how these blooms affect fish and, more broadly, marine ecosystems. Some benefits of jellyfish to marine fish include provisioning of food for some species and shelter for juvenile stages of several others. There is also a relatively minor human benefit in that some jellyfish are both commercially fished and cultured for human consumption in several countries. However, the negative effects of jellyfish population outbursts are thought to greatly exceed any positive ones and their effects on ecosystems and the economies that depend on them can be profound. These effects have been examined through field studies, controlled laboratory experiments, and estimated using quantitative ecosystem models. Jellyfish are generally detrimental to fish because they feed on zooplankton and ichthyoplankton, and so are both predators and potential competitors of fish. Relatively little of the energy consumed by gelatinous zooplankton ends up at higher trophic levels of interest to humans compared to krill and forage fishes. Jellyfish blooms also directly impact commercial fisheries through filling or clogging trawls and fouling fixed gear and aquaculture net pens, resulting in enormous economic losses worldwide. This session will focus on empirical field, laboratory, or modeling studies that examine the effects jellyfish have on marine ecosystems, fish species and fisheries, and relevant ecosystem-based management issues important to the needs of society over wide-ranging space and time-scales up to and including climate variations.

PICES Twenty-first Annual Meeting (PICES-2012)
October 12–21, 2012
Hiroshima, Japan

Working Group 26 on *Jellyfish Blooms around the North Pacific Rim: Causes and Consequences*

The second meeting of PICES WG 26 (*Jellyfish Blooms around the North Pacific Rim: Causes and Consequence*) was held October 14, 2012, in Hiroshima, Japan. The meeting was chaired by Dr. Shin-ichi Uye and Dr. Richard Brodeur. The third Co-Chair, Dr. Won-Duk Yoon, was not able to attend. A new Japanese WG member, Dr. Masaya Toyokawa, met with the group for the first time. All PICES member countries were represented at the WG meeting and many prominent jellyfish scientists from ICES member countries also attended and provided useful comments and suggestions. A total of 12 members and 11 observers participated in the meeting (*WG 26 Endnote 1*). The agenda for the meeting can be found in *WG 26 Endnote 2*.

AGENDA ITEM 3
Report on the preparation of the S7: BIO/FIS Topic Session

A brief report on the preparation for, and status of, the 2012 Topic Session on "*Jellyfish in marine ecosystems and their interactions with fish and fisheries*" was presented. The Convenors (Drs. Brodeur, Uye, Yoon, and Song Sun of PICES) and their ICES Co-convenors from Europe (Dr. Chris Lynam of the UK and Dr. Corneila Jaspers of Denmark) received a large number of abstract submissions from the scientific community that filled the day-long session, along with a substantial number of posters. They also received commitments from Dr. Rejii Masuda of Japan, Dr. Monty Graham of the U.S., and Dr. Thomas Doyle of Ireland to present as invited speakers.

AGENDA ITEM 4
Fourth International Jellyfish Bloom Symposium

A request was made by the WG Chairs for PICES sponsorship of the Fourth International Jellyfish Bloom Symposium to be held in Hiroshima, Japan, in June 2013. The request was for travel assistance for 1 or 2 invited speakers. It was decided that the WG would hold a one-day inter-sessional meeting in advance of the symposium to take advantage of the expertise coming to the meeting, including present WG members.

AGENDA ITEM 5
WG report outline and brief report on the current status of writing, and coordination of jellyfish sampling techniques

The remainder of the meeting consisted of discussions on the current state of writing for the WG final report. After brief discussions, the WG made slight modifications to the outline of the report adding several new sections that were deemed useful. The major sections of the WG report are as follows: 1) Introduction and purpose, 2) Life history and population dynamics, 3) Sampling considerations, 4) Spatio-temporal variations of biomass and current bloom conditions in regional seas, 5) Physio-ecological properties, 6) Impacts on marine ecosystems and socio-economics, 7) Reducing jellyfish impacts, and 8) Conclusions and prioritized recommendations for future research. WG members were assigned to each of these sections and the status of writing was presented. Discussions were carried out on how this report might best address the goals and themes of the FUTURE program.

AGENDA ITEM 6
Jellyfish sampling techniques

Presentations were made on four different aspects of sampling methodology (trawling, video, acoustics, sonar imaging) used within PICES for assessment of abundance of jellyfish.

AGENDA ITEM 7
Report on new topics

In a separate but related activity, many of the WG members met with a group of scientists planning to construct ecosystem models for many regions heavily impacted by jellyfish. This project plans to put together holistic ecosystem models for three PICES regions (California Current, Eastern Bering Sea, and ocean off Japan) as well as two non-PICES regions (Gulf of Mexico and Humboldt Current) in the coming years and examine the impact jellyfish have on trophic structure, particularly related to their effect on forage fishes. This work will likely contribute useful information to the management of these ecosystems in the future.

WG 26 Endnote 1

WG 26 participation list

Members

Mary Arai (Canada)
Richard Brodeur (USA, Co-Chairman)
Lucas Brotz (Canada)
Siqing Chen (China)
John Field (USA)
Haruto Ishii (Japan)
Jennifer Purcell (USA)
Kyoungsoon Shin (Korea)
Masaya Toyokawa (Japan)
Shin-ichi Uye (Japan, Co-Chairman)
Zijun Xu (China)
Alexander Zavolokin (Russia)

Observers

Sonia Batten (Canada)
Ik Kyo Chung (Korea)
Ryuji Furukawa (Japan)
Cornelia Jaspers (Denmark)
Martin Lilley (France)
Chris Lynam (UK)
Ryosuke Makabe (Japan)
Alenka Malej (Slovenia)
Chiaki Mizota (Japan)
Yasunori Watanabe (Japan)
Fu Zhilu (China)

WG 26 Endnote 2

WG 26 meeting agenda

1. Opening remarks
2. Introduction of a new member (Masaya Toyokawa, who has replaced the former Japanese member, Hideki Akiyama)
3. Brief report on the preparation of the S7: BIO/FIS Topic Session (1-day) on "*Jellyfish in marine ecosystems and their interactions with fish and fisheries*"
4. Proposal of the involvement of PICES in the Fourth International Jellyfish Bloom Symposium
5. Change in the WG report outline and brief report on the current status of writing
6. Discussion about coordination of jellyfish sampling techniques
7. Brief report on new topics and achievements in jellyfish bloom research in each country
8. Closing remarks

Extracted from:

Summary of Scientific Sessions and Workshops at PICES-2012

BIO/FIS Topic Session (S7)
Jellyfish in marine ecosystems and their interactions with fish and fisheries

Co-sponsored by: *ICES*

Co-convenors: *Richard Brodeur (PICES/USA), Cornelia Jaspers (ICES/Denmark), Christopher Lynam (ICES/UK), Song Sun (PICES/China), Shin-Ichi Uye (PICES/Japan) and Won-Duk Yoon (PICES/Korea)*

Background

Evidence is accumulating that gelatinous zooplankton populations have increased substantially in many regions of the world, most likely through anthropogenic stresses, but we have insufficient understanding of how these blooms affect fish and, more broadly, marine ecosystems. Some benefits of jellyfish to marine fish include provisioning of food for some species and shelter for juvenile stages of several others. There is also a relatively minor human benefit in that some jellyfish are both commercially fished and cultured for human consumption in several countries. However, the negative effects of jellyfish population outbursts are thought to greatly exceed any positive ones and their effects on ecosystems and the economies that depend on them can be profound. These effects have been examined through field studies, controlled laboratory experiments, and estimated using quantitative ecosystem models. Jellyfish are generally detrimental to fish because they feed on zooplankton and ichthyoplankton, and so are both predators and potential competitors of fish. Relatively little of the energy consumed by gelatinous zooplankton ends up at higher trophic levels of interest to humans compared to krill and forage fishes. Jellyfish blooms also directly impact commercial fisheries through filling or clogging trawls and fouling fixed gear and aquaculture net pens, resulting in enormous economic losses worldwide. This session focused on empirical field, laboratory, and modeling studies that examine the effects jellyfish have on marine ecosystems, fish species and fisheries, and relevant ecosystem-based management issues important to the needs of society over wide-ranging space and time-scales up to and including climate variations.

Summary of presentations

Studies presented at this meeting indicate that ecosystem degradation in diverse systems such as the Irish Sea, Sea of Japan, and Gulf of Mexico, coupled with climatic changes, can be linked to elevated jellyfish abundances. Some synchrony in jellyfish time-series was evident across the world's oceans, in particular between such seemingly unrelated systems as the Adriatic Sea and Inland Sea of Japan. More co-ordinated research effort is necessary to substantiate these general observations and future collaborations between Pacific and Atlantic scientists were discussed, including the possibility of a joint ICES/PICES Working Group.

While climate trends were clear in many of the data sets presented, it is still highly debated which factors and mechanistic processes drive the observed variability in gelatinous zooplankton biomass between the years and decades. Several examples highlighted the relationship between fish landings, their historic reduction due to overfishing and subsequent trends of increasing jellyfish populations. This indicates an indirect interaction between fishing impacts and jellyfish biomass and potentially of importance is the trophic level that the fisheries target. However, it was highlighted that for many years the willingness by fisheries management to consider indirect linkages of fisheries to gelatinous zooplankton has been limited.

Many risks (from reduced tourism to disruption to power plant coolant systems) associated with the threat of rising jellyfish populations were identified during the meeting and these risks should be communicated to managers and policy makers directly. If jellyfish population sizes are to be managed and outbreaks prevented, then the threat posed by jellyfish to fish, fisheries and other activities must be considered within the ecosystem approach to fisheries management.

An interesting approach to manage the consequences of giant *Nemopilema nomurai* blooms was presented where the implementation of diel vertical migration and temperature into a drift model study helped to accurately predict the dispersal of *N. nomurai* in the Sea of Japan, which is crucial information for the fishermen in the respective regions to prevent damage to their equipment.

The interaction between jellyfish and fish can be complex and include bottom-up and top-down pathways. Regarding bottom-up processes, several talks and posters addressed the reproduction potential in relation to hydrographical and environmental features. The polyp stage and/or egg production rates are critical factors determining the next generations' population size. In this context, the continued creation of artificial hard substrates is of paramount importance. Even a relatively small floating pontoon (6 × 48 m) recently installed in Japanese waters had been found to generate many million young medusoids within a year of installation. It was reported that a treatment to stop such biofouling was in development and shows some promise.

A notable example of the problem of biofouling by polyps on salmon aquaculture facilities, especially in northern Europe, was described. Polyp colonies grow on the cages and this commonly leads to salmon gill disorders and reduced aquaculture revenues. More dramatically, mass mortalities of salmon have occurred owing to jellyfish outbreaks drifting into salmon pens and technological developments (bubble nets, early warning systems) have been used to combat this problem. It was further shown that polyp settling is highly dependent on salinity and has been restricted to high saline areas in Chinese river runoff-influenced lagoons, thereby limiting their settling opportunities and reproductive potential. Similarly, salinity effects on reproduction rates have been documented to restrict the range expansion of the invasive ctenophore *Mnemiopsis leidyi*. This information could be used for determining site locations of large projects introducing artificial hard substrates (*e.g.*, windfarms) which might be better located in low salinity areas where polyp settling is restricted. However, in general bottom-up processes need to be further investigated and the monitoring of ephyra in addition to medusae should be conducted since they are commonly ignored in zooplankton investigations.

From a top-down aspect, it was addressed and experimentally confirmed that many species of fish prey on jellyfish. For several fish species in Japanese waters, it has been shown that gelatinous food sources promote growth and in some cases, are even essential in the fish diet to sustain high growth rates. Similarly, certain commercially important salmon species (*e.g.*, chum salmon, *Oncorhynchus keta*) depend on a ctenophore diet during their development in the North Pacific. However, the responses are species-specific and much more research is required in this area. Gelatinous species are typically digested so rapidly that they can appear absent from the gut contents of fish even if the fish have fed on them within an hour. To avoid this problem, molecular and genetic tools for gut content analyses, especially for commercially important fish species, should be employed more often to confirm the extent of jellyfish and ctenophores in their diets. Diets of potential jellyfish predators should be examined on fresh material at sea whenever possible.

In conclusion, jellyfish threats to aquaculture, fisheries, tourism, and power generation are well known and the risks should be quantified. The trade-off between potential losses and the cost of mitigation should be considered and the acceptable risk levels evaluated. Ecosystem degradation and climatic changes alongside increased usage of the marine environment by man are likely to stimulate further outbreaks of gelatinous zooplankton populations and detrimental impacts by jellyfish may become more common. The development of the ecosystem approach to fisheries management provides a framework in which to address and tackle these issues.

List of papers

Oral presentations

William M. Graham, Stefan Gelcich, Carlos M. Duarte, Shin-ichi Uye, Richard Brodeur, Robert H. Condon and NCEAS Jellyfish Working Group (Invited)
Jellyfish and fisheries: Risks, trade-offs and adaptations

Thomas K. Doyle, Emily J. Baxter, Graeme C. Hays, Hamish D. Rodger and Neil M. Ruane (Invited)
Detrimental impacts of jellyfish on finfish aquaculture: insights from the North East Atlantic

Reiji Masuda, Yuko Miyajima, Ryosuke Ohata and Yoh Yamashita (Invited)
Jellyfish as a predator and prey of fishes: Underwater observations and rearing experiments

Jennifer E. Purcell, Ana Sabatés, Verónica Fuentes, Francesc Pagès, Uxue Tilves, Alejandro Olariaga and Josep-María Gili
Predation potential of blooming jellyfish, *Pelagia noctiluca*, on fish larvae in the NW Mediterranean Sea

Cornelia Jaspers
The invasive ctenophore *Mnemiopsis leidyi* in northern European waters and its potential impact on fisheries

Shin-ichi Uye, Alenka Malej and Tjasa Kogovsek
Comparative analysis of the Inland Sea of Japan and the northern Adriatic: Can changes in anthropogenic pressures disclose jellyfish outbreaks?

Martin K.S. Lilley, Steven E. Beggs, Thomas K. Doyle, V.J. Hobson, K.H.P. Stromberg and Graeme C. Hays
Direct and indirect evidence for massive differences in jellyfish biomass between the Pacific and Atlantic: Implications for fisheries bycatch?

Lucas Brotz, William W.L. Cheung, Reg Watson, Kristin Kleisner, Evgeny Pakhomov, Philippe Cury, Roxane Maranger, Brooke Campbell and Daniel Pauly
Anthropogenic impacts related to observed increases of jellyfish populations

Christopher P. Lynam, Martin K.S. Lilley, Thomas Bastian, Thomas K. Doyle, Steven E. Beggs and Graeme C. Hay
Have jellyfish in the Irish Sea benefited from climate change and overfishing?

Alexander V. Zavolokin
Jellyfish of the Far Eastern Seas of Russia: Composition, spatio-temporal variations and significance for ecosystems

Song Sun, Chaolun Li, Guangtao Zhang, Shiwei Wang and Xiao Xia Sun
Giant jellyfish blooms in the Yellow Sea and East China Sea

Akira Okuno, Tatsuro Watanabe, Satoshi Kitajima, Naoto Honda and Katsumi Takayama
Numerically simulated migration/distribution of *Nemopilema nomurai* in the Japan Sea using temperature-based controls

Masaya Toyokawa, Akira Yasuda, Yusuke Murata, Kazuhiro Aoki, Manabu Shimizu and Minoru Hamada
Aurelia swarms originate from polyps near the mouth of a bay: evidence from Mikawa Bay and Ise Bay

Mary Needler Arai
Predation on gelatinous cnidaria and ctenophores

Brian E. Smith and Jason S. Link
The presence of gelatinous zooplankton in the diets of fishes of the Northeast U.S. continental shelf: Trends in shelf-wide feeding and consumptive removals

James J. Ruzicka, Elizabeth A. Daly and Richard D. Brodeur
Salmon and jellyfish: Bumping elbows in the Northern California Current

John C. Field Jarrod A. Santora Keith Sakuma Amber Payne and Baldo Marinovic
Spatial and temporal patterns of variability in Scyphomedusae in the central California coastal marine ecosystem

Richard D. Brodeur, Mary Beth Decker, Elizabeth A. Daly, Caren Barcelo, James J. Ruzicka and Kristin Cieciel
A tale of two *Chrysaora*: Pivotal roles in contrasting marine ecosystems

Poster presentations

Sim Yee Kwang, Chuah Chern Chung, Anita Talib and Khairun Yahya
Exogenous impacts on the massive occurrence of jellyfish in the northern part of Malacca Straits, Malaysia

Wen-Tseng Lo, Hung-Yen Hsieh and Shwu-Feng Yu
Comparison of siphonophore assemblages during northeasterly and southwesterly monsoon seasons in the Taiwan Strait, western North Pacific Ocean

Ryosuke Makabe, Ryuji Furukawa, Mariko Takao and Shin-ichi Uye
Marine construction as a factor boosting *Aurelia aurita* s.l. blooms: A case study of a new floating pier deployment in Hiroshima Bay, Japan

Takashi Kamiyama
Planktonic ciliates as a prey source for moon Jellyfish *Aurelia aurita*: Feeding activities and growth effects of ephyra and metephyra stages

Satoshi Kitajima, Akira Okuno, Naoki Iguchi, Naoto Honda, Tatsuro Watanabe and Osamu Katoh
Low temperature excludes medusae of *Nemopilema nomurai* in the Japan Sea in winter

Thomas Bastian, Damien Haberlin, Mary Catherine Gallagher, Sean Rooney, Graeme C. Hays and Thomas K. Doyle
Tracking the lion's mane jellyfish: Horizontal and vertical movements of *C. capillata* (Scyphozoa) in a shallow coastal environment

Steven E. Beggs, Thomas Bastian, Martin K.S. Lilley and Thomas K. Doyle
Annual and regional variations in associations between Scyphomedusae and juvenile gadoids in the Irish Sea

Martin K.S. Lilley and F. Lombard
Developing a technique for *in-situ* monitoring of fragile planktonic organisms

Kristin Cieciel, Jeanette Gann and Bruce Wing
Methods for conducting individual measurements on trawled jellyfish

Naoki Fujii, Shinya Magome, Atsushi Kaneda and Hidetaka Takeoka
Relationship between jellyfish abundance and environmental fluctuations in Uwa Sea

Jun Nishikawa, Fatimah Md. Yusoff, Nguyen Thi Thu, Khwanruan Srinui, Mulyadi and Shuhei Nishida
Jellyfish fisheries in Southeast Asia

PICES Twenty-second Annual Meeting (PICES-2013)
October 11–20, 2013
Nanaimo, Canada

Working Group 26 on *Jellyfish Blooms around the North Pacific Rim: Causes and Consequences*

The third meeting of PICES WG 26 (*Jellyfish Blooms around the North Pacific Rim: Causes and Consequence*) was held inter-sessionally in Hiroshima, Japan, (June 4, 2013) before the Fourth International Jellyfish Blooms Symposium in early June. The meeting was chaired by Dr. Shin-ichi Uye and Dr. Richard Brodeur. A new Korean WG member, Dr. Seungshic Yum, met with the group for the first time. All PICES member countries were represented at the WG meeting and several prominent jellyfish scientists from non-PICES nations also attended and provided useful comments and suggestions. A total of 11 members attended the WG meeting. PICES co-sponsorship of the Jellyfish Blooms Symposium was acknowledged which allowed for funding support for two invited speakers (Drs. Larry Madin and Rob Condon) to present at the meeting (*WG 26 Endnote 1*). The WG proposed a theme session to be held at the PICES FUTURE Open Science Meeting in Hawaii (April 15–18, 2014) entitled "*Natural and anthropogenic drivers of jellyfish blooms in coastal ecosystems: Correlation, causation, and prediction*" to be co-convened by WG members Uye, Brodeur and Lucas Brotz. The proposal was reviewed by Science Board and it was recommended that instead of being a separate session, this topic should be merged with another session on "*Identifying multiple pressures and system responses in North Pacific marine ecosystems*" led by Dr. Ian Perry. Discussions are underway with the organizers of that session to integrate jellyfish research into this theme session.

The remainder of the meeting consisted of discussions on the current state of writing for the WG report. Over the last twelve months, the WG members have been researching and writing their sections for the report and numerous emails have been exchanged among members. Progress by the different WG members was presented along with updates of the status of bloom conditions in several PICES regions. After brief discussions, the WG made slight modifications to the outline of the report, adding several new sections that were deemed useful to include. The major sections of the WG report are as follows:

1) Introduction and purpose,
2) Life history and population dynamics,
3) Sampling considerations,
4) Spatio-temporal variations of biomass and current bloom conditions in regional seas,
5) Physio-ecological properties,
6) Impacts on marine ecosystems and socio-economics,
7) Reducing jellyfish impacts, and
8) Conclusions and prioritized recommendations for future research.

Discussions were included on how this report may best address the goals and themes of the FUTURE program.

During the past summer, WG Co-Chair, Dr. Brodeur, worked with two ICES colleagues (Cornelia Jaspers of Denmark and José Luis Acuña of Spain) to put together a proposal for a joint ICES/PICES session on jellyfish at the next ICES Annual Meeting to be held in A Coruña, Spain, in September 2014 (see *WG 26*

Endnote 2 for title and description). This is a followup to the very successful PICES/ICES collaborative session held at the 2012 PICES Annual Meeting in Hiroshima, Japan. In contrast to the one in 2012, this session would focus on the socio-economic impacts of blooms on humans, particularly related to fisheries. The other WG Co-Chair, Dr. Uye, was proposed as a keynote speaker for this session. ICES reviewed the proposal at their September annual meeting and ranked it as the top proposed session so it is likely to be approved for the next meeting. The WG will next request sponsorship by the BIO and FIS committees prior to moving forward to Science Board for consideration.

Finally, due to circumstances beyond their control, neither WG Co-Chair was able to attend the proposed WG business meeting at the 2013 PICES Annual Meeting in Nanaimo, Canada, so the meeting was cancelled. It was suggested instead that the WG members continue to write their reports and submit them to the WG Chairs.

WG 26 Endnote 1

Report on International Jellyfish Blooms Symposium in PICES Press

https://www.pices.int/publications/pices_press/volume21/v21-n2/pp_14-15_Jellyfish-Symposium.pdf

WG 26 Endnote 2

Proposal for joint 1-day ICES/PICES Topic Session on
"*Gelatinous zooplankton on a global perspective: interactions with fisheries and consequences for socio-economics*"

Convenors: José Luis Acuña (Spain, ICES), Richard Brodeur (USA, PICES), Cornelia Jaspers (Denmark, ICES)

Proposed Invited speaker: Shin-Ichi Uye (Japan)

Gelatinous zooplankton, such as ctenophores, jellyfish and pelagic tunicates, contain groups belonging to the fastest growing metazoans on Earth, contributing more to secondary production than crustacean zooplankton during periods in certain regions. Irrespectively, gelatinous zooplankton remain understudied and disregarded in most food web investigations and are largely viewed as a dead end in the food chain. Lately, evidence has accumulated that gelatinous zooplankton populations have increased and likely have benefitted from global change. Further, anthropogenic stressors such as eutrophication, bio-invasions and overfishing have been correlated with increased jellyfish and ctenophore abundances with documented changes in food web structure, functioning and productivity of many marine ecosystems around the world. Especially in the Mediterranean Sea, the Black Sea, the East Asian marginal seas, the Benguela Current, and fjord systems around northern Europe, bio-invasions and blooms of gelatinous zooplankton have gained public attention, with documented shifts in the food web structure, functioning and corresponding socio-economic consequences for fisheries and tourism. This theme session aims at addressing the role, position and importance of gelatinous zooplankton organisms for marine ecosystems and their impact on food web structure, functioning and overall productivity.

We encourage presentations on gelatinous zooplankton and their:

- spatial and temporal distribution patterns
- contributions to carbon cycling in pelagic & benthic ecosystems including higher trophic levels
- population dynamics or species interactions of native and invasive groups
- socio-economic impacts e.g. on fisheries, aquaculture and tourism
- potential as a fast growing, renewable resource

ICES 2014 Annual Science Conference

September 22–26, 2014

A Coruña, Spain

ICES/PICES Theme Session A

Gelatinous zooplankton on a global perspective: interactions with fisheries and consequences for socio-economics

Conveners: Cornelia Jaspers, Denmark (coja@aqua.dtu.dk), Richard Brodeur, USA, PICES (rick.brodeur@noaa.gov), and José Luis Acuña, Spain (acuna@uniovi.es)

Theme session A on gelatinous zooplankton at the ICES Annual Science Conference 2014 in Spain attracted a large number of high quality research contributions from 18 different countries such as Japan, Taiwan, Mexico, Russia, Israel, Australia, the US and Europe, which materialized into 29 oral and 16 poster presentations during the 1.5 day session. The high quality of presented research at this special theme session is underlined by the fact that two out of four presentation awards were given to young scientists from this session. The theme session was co-sponsored by PICES and was as such a follow up to the joint ICES/PICES session on jellyfish–fish interactions held at the PICES Annual Meeting in Hiroshima, Japan in 2012.

Gelatinous zooplankton (GZ) is a collective term for a taxonomically and functionally diverse group of organisms whose bodies are significantly more watery than those of other classical zooplankton such as crustaceans. Members of the GZ – which include medusoid and siphonophore cnidarians, comb jellies and tunicates among others – exhibit brisk population dynamics leading to so-called blooms with the potential to interfere with ecosystem function, and impact fisheries, aquaculture and tourism. The main goal of this special theme session was to address the role and contribution of gelatinous zooplankton to the carbon cycling and productivity of pelagic ecosystems, especially to higher trophic levels such as fish, and their impact on socio-economics (*e.g.*, jellyfish bloom formations due to bio-invasions, eutrophication, overfishing and impact on aquaculture and tourism).

The possibility that global change, overfishing, eutrophication, and other anthropogenic factors may be driving the oceans towards a "more gelatinous future" has stimulated research into the global distribution and long term trends of GZ biomass, a research focus exemplified by the global database of jellyfish records (JEDI) and the large regional coverage in this session. Contributions dealt with spatial and temporal variability of GZ biomass ranging from the North, Baltic, Mediterranean, Bering and Barents Seas to Australian and Japanese coastal waters, Southern as well as northern Gulf of Mexico and the northern California Current. Methodological approaches included not only classical sampling techniques but also promising technological advances with a presented *in situ* visualization tool allowing for micro-scale investigations of gelatinous zooplankton which are important to dismantle thin layer accumulation and distribution patterns across frontal systems. This highlights that new approaches like camera systems should be incorporated into monitoring activities and field investigations to appropriately sample all spatial and temporal scales of the food web. A large set of presentations was devoted to address the distribution and impact of particularly problematic species like invasive or stinging groups (i.e. scyphozoan and box jellyfish) and their direct impact on tourism, fisheries and aquaculture. From this session it became apparent that the mauve stinger *Pelagia noctiluca* is of particular importance for the Mediterranean Sea ecosystem. Contributions showed the potential of the mauve stinger to decimate populations of fish eggs and larvae, their detrimental effects on caged gilthead sea bream and offered a first glance at the lifetime vital statistics of this holoplanktonic species since it was successfully cultured from egg to adult. Detailed studies on jellyfish fish interactions are sparse but apart from direct predation on fish recruits and interactions due to tissue damage and mass mortality in marine farmed fish, jellyfish can also be an important food source. Results were presented where fish species like the *Boops boops* explicitly preyed on the mauve stinger *P. noctiluca*, and a second fish species, *Saparus aurata* preyed on all life stages of the moon jelly *Aurelia aurita*. However, *in situ* gut content analyses showed that *ca*. 20% of the adult *P. noctiluca* diet consists of fish eggs. Further, night surveys in the Ligurian Sea demonstrated that the jellyfish biomass is considerably higher than commercial fish species with a maximum estimated *P. noctiluca* biomass of 100–300 tons km^{-2}. Therefore, the direct predation impact of *P. noctiluca* on fish populations can be substantial, especially for regions where a large spatial and temporal overlap between fish recruits and jellyfish occurs. All these studies seem to respond to a growing concern of the potential threat of *P. noctiluca* to Mediterranean fisheries, aquaculture and tourism. But problems with the mauve stinger are not only of importance in the Mediterranean Sea but also in parts of northern Europe since severe impacts have been reported on marine salmon farms in the Irish Sea, where blooms lead to a mass mortality and several million Euro loss for the aquaculture industry. Further, the geographic range is expected to expand due to climate change highlighting that interactions between stinging jellyfish and aquaculture are expected to increase. Hence, detailed population dynamic investigations of bloom forming, stinging jellyfish species are needed to allow for establishment of a warning system for fishermen, like has been established for the NW Mediterranean Sea and in Japanese waters.

Gelatinous zooplankton population dynamics are complex and require understanding of bottom-up and top-down pathways. Regarding bottom-up processes, several contributions addressed jellyfish reproduction potential in relation to hydrographical and environmental features including drift models for estimating the dispersal of recruits. The polyp stage and/or egg production rates are critical factors determining the future population size. In this context, examining the effects of the continued addition of artificial hard substrates necessary for polyp attachment is of paramount importance and it has been shown that 90% of the polyps of the moon jellyfish settled as secondary biofouling on *e.g.*, oyster shells from mariculture farms in an enclosed lagoon system in the Mediterranean Sea.

A dramatic example of interference between gelatinous zooplankton bloom and fish-eries was offered by the invited speaker, Prof. Shin-Ichi Uye from Hiroshima University, who reviewed the threat posed by jellyfish to fisheries in the Sea of Japan and adjacent coastal areas while demonstrating science-based mitigation practices which have saved the fishing industry several hundred million Euros annually.

Direct predation on fish eggs and larvae as well as competition for the same food lead to a complex interaction between jellyfish and fish; however, the detailed pathways whether it leads to either a fish-dominated or a jellyfish-dominated food web still remain hypothetical. Time series analyses from different regions of the world's oceans showed that jellyfish overlap with fish in space and time and that jellyfish and forage fish share the same prey field (*e.g.*, Gulf of Mexico, Bering Sea, Barents Sea, Northern California Current). This leads to an observed pattern of jellyfish–forage fish replacement cycles. Cross-ecosystem comparison of the above mentioned systems shows that jellyfish have a large footprint but a small reach component, leading to a low production available for higher trophic levels, while forage fish have a relatively small footprint and a large reach component, leading to higher transfer efficiencies up the food web. Hence, forage fish have an up to 270 times larger reach/footprint ratio highlighting their importance as an energy pathway compared to jellyfish. Interestingly, different fishing scenarios were tested and a no-fishing model run in three different ecosystems led to an increase in fish biomass with similar reduction in jellyfish biomass. Also it is interesting to note that modelling frameworks are now moving into the direction of incorporating different gelatinous zooplankton groups. For example, the latest results of an Ecopath model were presented where three different functional gelatinous zooplankton groups were included, namely large carnivorous jellies, small gelatinous carnivorous and filter-feeders. Energy transfer metrics showed an order of magnitude difference in the fraction of energy available for higher trophic levels compared to the footprint ratio between jellyfish and fish. Further, a presented competition model has given another line of evidence for a more gelatinous future. Empirical relationships between secchi-depth as proxy for eutrophication, jellyfish and fish biomass suggest that the lower the visibility, the lower the pelagic fish biomass and the higher the jellyfish abundances. However, further empirical evidence is necessary to enlighten the detailed dynamics.

Regarding the socio-economic perspective of gelatinous zooplankton blooms, our second invited speaker, Dr. Veronica Fuentes from Spain, presented recent advances in understanding jellyfish population dynamics and socio-economic consequences of jellyfish blooms. In the Mediterranean Sea, a recent increase in abundances of the mauve stinger, the Portuguese Man-of-War and a box jellyfish has led to increased encounter with the negative side of gelatinous zooplankton. For example, 60% of all injuries treated along the Spanish Mediterranean coast in 2012 were associated with jellyfish such as stings of the box jellyfish *Carybdea marsupialis*. Fuentes and co-workers have established a tight coupling between society and scientific community including public outreach activities and a platform for jellyfish sightings. A highly relevant tool in this context is the newly established jellyfish beaching information system. This system is based upon sighting information, monitoring activities, detailed knowledge about population dynamics of bloom forming species, and a new modelling framework which allows predicting species distributions to alarm authorities about beaches which are likely to suffer from jellyfish beachings.

Presentations showed that on a global scale the biomass of jellyfish has exceeded the biomass of small pelagic fish in several regions. Furthermore, it was shown that climatic changes can be linked to elevated jellyfish abundances with synchrony in jellyfish time-series evident across the world's oceans. While climate change signals were clear in many of the data sets presented, it is still highly debated which factors and mechanistic processes drive the observed variability in gelatinous zooplankton biomass between years and decades. Some studies highlighted the relationship between fish landings, their historic reduction due to overfishing and subsequent trends of increasing jellyfish populations. This indicates an indirect interaction between fishing impacts and jellyfish biomass, potentially suggesting competition between jellyfish and the trophic level that the fisheries target (*i.e.*, forage fishes). Though the causal relationships remain unclear, experimental results from this session confirm that direct competition effects between jellyfish and fish along with human impacts driving survival and reproduction of jellyfish (*e.g.*, adding hard substrate and increased eutrophication levels) are important in understanding jellyfish population dynamics and the formation of blooms. Many risks (from reduced tourism to clogging of power plant coolant systems) associated with the threat of rising jellyfish and gelatinous zooplankton populations were identified during this session and these risks should be communicated to managers and policy makers directly. One presentation even highlighted the importance of public outreach and social media in communicating jellyfish science to a wider audience. If gelatinous zooplankton, in general, and jellyfish populations, in particular, are to be managed and their outbreaks prevented or mitigated, then the threat posed to fish, fisheries and other activities must be considered within an ecosystem approach to fisheries management. We have seen some attempts to do so in this session and hope that new results presented here will foster those approaches.

In conclusion, jellyfish and gelatinous zooplankton threats to aquaculture, fisheries, tourism, and power generation are well known but the risks need to be better quantified. The trade-off between potential losses and the cost of mitigation should be considered and the acceptable risk levels evaluated. Ecosystem degradation and climatic changes alongside increased usage of the marine environment by man are likely to stimulate further outbreaks of gelatinous zooplankton populations and detrimental impacts by jellyfish may become more common. The development of an ecosystem approach to fisheries management provides a framework in which to address these issues.

Based on the large interest which this session attracted, it is evident that gelatinous zooplankton, in general, and jellyfish, in particular, are an important research compo-nent within the ICES/PICES community. But further multinational research effort needs to be devoted towards developing a mechanistic understanding of jellyfish and gelatinous zooplankton blooms, including environmental factors leading to their rise.

Finally, the conveners from Theme Session A on gelatinous zooplankton have arranged for selected papers to be submitted to a special issue in *Journal of Plankton Research* devoted to this session theme and encourage authors to submit manuscripts.

ICES Early Career Scientist awards

Early career scientist award recipients at ICES 2014ASC: Jessica Luo (left) and Raquel Marques with SCICOM Chair, Yvonne Walther

Best presentation

Jessica Luo
Rosensteil School of Marine and Atmospheric Sciences, University of Miami, USA

Environmental drivers of the fine-scale distribution of gelatinous zooplankton across a meso-scale front

"This powerful new sampling technology allows predator prey dynamics including gelatinous animals to be investigated. Examples presented included impressive images and observations of community structure at fronts and of environmental drivers associated with zooplankton taxa."

International Council for the Exploration of the Sea (ICES)

Best presentation

Raquel Marques
University of Algarve, Portugal

Dynamics of production and mortality of Aurelia aurita's ephyrae in Thau Lagoon, Northwestern Mediterranean

"Sophisticated and compelling presentation. Impressive amount of work, spanning *in situ* observations and laboratory experiments. Jellyfish populations might be controlled by fish predation."

International Council for the Exploration of the Sea (ICES)

Appendix 4

Publications Related to WG 26

Selected papers from the 2006 PICES Annual Meeting Topic Session on "*The human dimension of jellyfish blooms*"

Guest Editors: H. Iizumi and H. Ishii

https://www.jstage.jst.go.jp/browse/pbr/3/Supplement/_contents

Selected papers from the ICES 2015 ASC Theme Session on "*Gelatinous zooplankton on a global perspective: interactions with fisheries and consequences for socio-economics*"

https://academic.oup.com/plankt/issue/37/5

New PICES Jellyfish Working Group Formed

by Richard Brodeur and Shin-ichi Uye

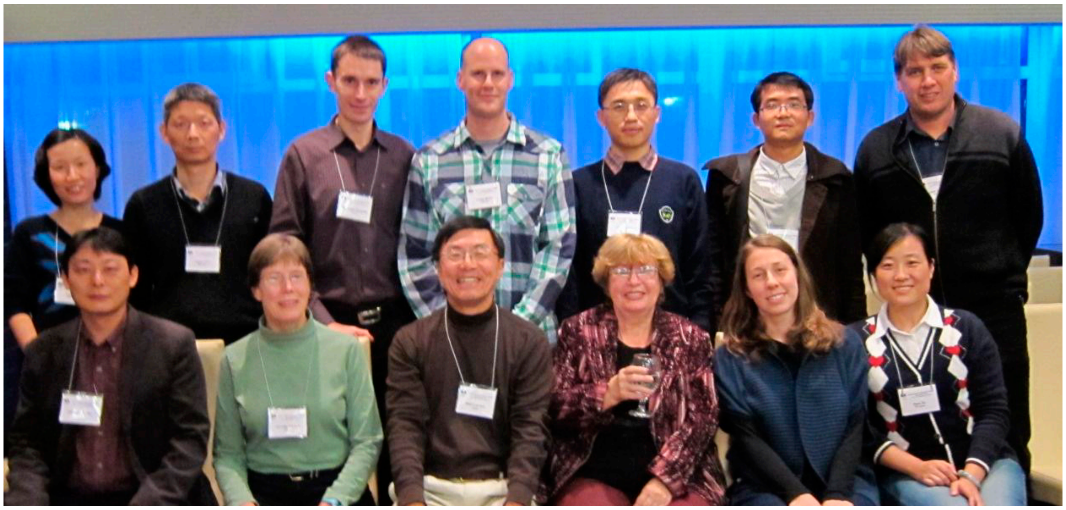
Similar to many other regions in the world, the North Pacific Ocean and surrounding marginal seas have experienced high numbers of jellyfish in recent years, culminating in massive blooms in some coastal areas. This region is among the most productive in the world in terms of fisheries catch, and many millions of people, especially those living in Asia, are dependent on the ocean for their nutritional needs. Scientists and managers have become increasingly concerned about the potential rise in the prevalence and magnitude of jellyfish blooms in recent years, and their potential impact on ecosystem services such as fisheries, tourism, and power generation. PICES has long recognized the importance of gelatinous zooplankton in marine ecosystems and the present limitations to our understanding of what initiates and maintains the blooms and their effects on other marine resources, and scientists from PICES member countries plan to work together to promote understanding and propose solutions to problems affecting the North Pacific. At the 2010 PICES Annual Meeting, a new Working Group on *Jellyfish Blooms around the North Pacific Rim: Causes and Consequence* was established with the explicit goal of bringing together experts from the member countries to address this issue and come up with potential solutions to reverse the increasing trend in jellyfish blooms in coastal waters. The terms of reference and the membership of the Group can be found at http://www.pices.int/ members/working_groups/wg26.aspx.

The Working Group met for the first time this past October in Khabarovsk (Russia), in conjunction with the 2011 PICES Annual Meeting. Fourteen out of 20 Working Group members attended this inaugural meeting. In order to grasp the general status of the jellyfish blooms around the North Pacific Rim, information about current and past jellyfish blooms and related research was presented for each member country.

Lucas Brotz (University of British Columbia, Canada), found that jellyfish have fluctuated over recent decades but have not shown any significant increases in Canadian Pacific coastal waters. He followed this with a presentation on trends in global jellyfish blooms, based on various sources of information from scientific literature to mass media articles. His results suggest that jellyfish have increased globally in recent decades with some certainty in about 70% of 64 Large Marine Ecosystems of the world, and these increases seem to be related to human impacts.

China currently runs two big national projects on jellyfish blooms. Siqing Chen (Yellow Sea Fisheries Research Institute) described the project on "*Key Processes, Mechanism and Ecological Consequences of Jellyfish Bloom in Chinese Coastal Waters*" that aims to understand the causes of jellyfish blooms in Chinese waters and their impacts on the ecosystem. Zijun Xu (North China Sea Environmental Monitoring Center, State Oceanic Administration) explained another project, focusing mainly on the establishment of a monitoring system for early warning of possible jellyfish blooms and determining techniques for minimizing their impacts on human society.

Japanese waters are substantially affected by jellyfish blooms, most intensively by the moon jellyfish *Aurelia aurita* and the giant jellyfish *Nemopilema nomurai*. Japanese scientists are examining the jellyfish problems under two major projects. Hideki Akiyama (Seikai National Fisheries



Group photo taken during a banquet after the 2011 Working Group 26 meeting. Front row from left: C. Han (Korea), J. Purcell (U.S.A.), S. Uye (Japan), E. Dulepova (Russia), K. Cieciel (U.S.A.) and Z. Xu (China). Back row from left: G. Liu (China, non-member), S. Chen (China), A. Zavolokin (Russia), L. Brotz (Canda), X. Pu (China), Y. Xu (China, non-member) and J. Field (U.S.A.). Missing from photo: H. Akiyama and H. Ishii (Japan).

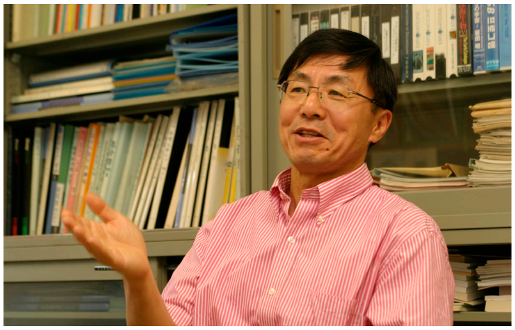
Research Institute) reported on the China-Japan-Korea International Giant Jellyfish Bloom Project, which includes a monitoring component and development of predictive indices. Shin-ichi Uye (Hiroshima University) summarized the results from the project entitled "*Studies on Prediction and Control of Jellyfish Outbreak*" (STOPJELLY), which aims to understand factors leading to the blooms, predict their severity, and develop chemical and biological methods to control jellyfish populations.

Representing Korea, Changhoon Han (National Fisheries Research and Development Institute) explained that his country is also suffering from jellyfish blooms, with a total economic loss of $265 million US in an intense bloom year. The Korean government has established a Jellyfish Monitoring and Countermeasure Center to tackle this problem and has initiated a program to minimize jellyfish damage to fisheries and tourism.

Alexander Zavolokin (Pacific Research Institute of Fisheries and Oceanography) reported that Russian scientists have been studying jellyfish (mainly taxonomic composition, abundance and biomass) since 1990 in the western Bering Sea, Okhotsk Sea and other Russian waters by trawl netting, sampling more than 10,000 stations in these regions. According to the results of their studies, the annual jellyfish biomass has fluctuated widely but did not show any consistent trends in the Bering Sea or Okhotsk Sea.

Jennifer Purcell (Shannon Point Marine Center, Western Washington University, U.S.A.) updated the jellyfish biomass in the eastern Bering Sea, where the jellyfish data have been consistently monitored since 1979. Biomass increased in the 1990s and declined substantially for 8 years after 2000, but has surged again since 2009. She also presented the geographical distribution of jellyfish along Puget Sound, where they are more abundant in waters adjacent to more populated cities, indicating some positive effects by human activity on jellyfish population increase. Finally, studies along the U.S. west coast were summarized, which have attempted to link jellyfish biomass with environmental changes.

The Working Group will be active for at least the next 3 years and is planning to sponsor symposia and workshops at future scientific meetings. A Topic Session on "*Jellyfish in marine ecosystems and their interactions with fish and fisheries*" has been proposed and approved by Science Board for the 2012 PICES Annual Meeting to be held in Hiroshima, Japan, and will be co-sponsored by ICES. The Working Group hopes to sponsor collaborative research cruises among PICES member countries in the future and suggest ways to adapt to, or control, jellyfish blooms. Anyone who has data from within the PICES study region to contribute to the Working Group report is welcome to contact members of the Group.



Dr. Richard Brodeur (Rick.Brodeur@noaa.gov) is a Research Fisheries Oceanographer working in the Fish Ecology Division of the Northwest Fisheries Science Center, NOAA Fisheries, and is based in Newport (Oregon, U.S.A.). Ric began his career working on early life history and recruitment dynamics of walleye pollock in the Gulf of Alaska and Bering Sea for the Alaska Fisheries Science Center and became interested in jellyfish following their dramatic increase in that ecosystem. He came to Oregon to work on habitat preferences and trophic ecology of juvenile salmon and other pelagic fishes as well as recruitment processes in marine fishes. He has published on a variety of topics ranging from satellite oceanography to fish bioenergetics to fisheries acoustics, but has focused much of his research on feeding and food web interactions in the pelagic ecosystem. Ric has been heavily involved in PICES, serving on several committees and expert groups and organizing a number of special sessions and workshops at past meetings. He serves now as a Co-Chairman of the PICES Working Group on Jellyfish Blooms around the North Pacific Rim: Causes and Consequence.

Dr. Shin-ichi Uye (suye@hiroshima-u.ac.jp) is a Professor of biological oceanography at Hiroshima University. He initially studied zooplankton production ecology through intensive research on the population dynamics and productivity of major copepod species in Japanese coastal waters. Around 1990, he noticed a significant increase of unhealthy copepods coated in jellyfish mucus, and then gradually shifted his research interest to jellyfish biology. Shin-ichi is now involved in two Japanese jellyfish research projects: Studies on Prediction and Control of Jellyfish Outbreak (STOPJELLY) and the China-Japan-Korea International Project on the Giant Jellyfish Bloom. He was former President of the Plankton Society of Japan (2001–2004) and former President of the World Association of Copepodologists (2005–2008). Shin-ichi was awarded the Oceanographic Society of Japan Prize in 2010 for his advancement of zooplankton research, particularly on their functional roles in coastal marine ecosystems. He now serves as a Co-Chairman of the PICES Working Group on Jellyfish Blooms around the North Pacific Rim: Causes and Consequence.

The Fourth International Jellyfish Bloom Symposium

by Shin-ichi Uye and Richard Brodeur

The participants of the 4th International Jellyfish Bloom Symposium (June 5–7, 2013, Hiroshima, Japan).

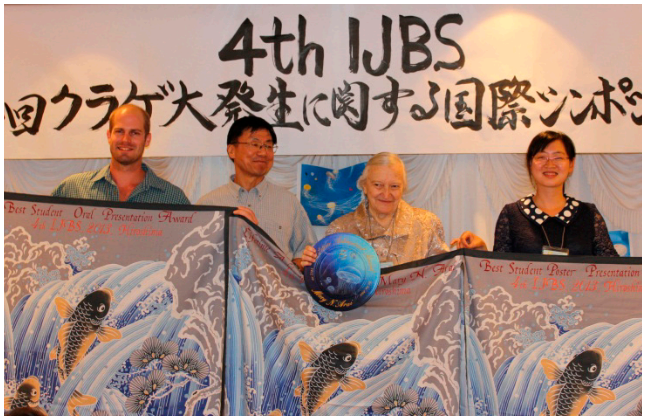
Following the initial meeting in Alabama (U.S.A.) in 2000, and subsequent meetings in Gold Coast (Australia) in 2008 and Mar del Plata (Argentina) in 2010, the 4th International Jellyfish Bloom Symposium was held June 5–7, 2013, in Hiroshima, Japan. Given the importance of jellyfish blooms to the North Pacific, PICES served as a co-sponsor of this event through its established Working Group on *Jellyfish Blooms around the North Pacific Rim: Causes and Consequence* (WG 26) and provided logistical and financial support for the symposium.

The symposium was a great success, attracting over 120 scientists from 29 countries and 5 continents. Following opening remarks by the symposium organizer and WG 26 Co-Chairman, Dr. Shin-ichi Uye (Hiroshima University, Japan), Dr. Larry Madin (Woods Hole Oceanographic Institution, U.S.A.) presented a comprehensive overview of the major taxonomic groups comprising this diverse group, along with a history of the sampling and utilization of jellyfish over time. He noted the importance of understanding the beneficial services that jellyfish provide to humans that are often overlooked in the media.

A second keynote talk given by Dr. Rob Condon (Dauphin Island Sea Laboratory, University of South Alabama, U.S.A.) described some of the progress achieved by the international Global Jellyfish Group sponsored by the National Center for Ecological Synthesis (NCEAS, U.S.A.) which completed its formal activities this past year. A key product of this working group was the establishment of the Jellyfish Data Initiative (JEDI), which provides a repository for most of the jellyfish historical abundance and distribution time series worldwide. Using this database, Rob led several studies examining the long-term trends in jellyfish blooms around the globe which not only indicate some recent increases in many regions, but also an underlying multi-decadal oscillation which inhibits drawing firm conclusions until the time series are suitably extended.

A final invited talk was provided by Dr. José Acuna (Oveido University, Spain) on the adaptations that jellyfish have evolved to make them efficient consumers in the marine environment on a similar scale as the fishes, despite being greater than 95% body water content. He also stressed the diversity of feeding modes in the gelatinous zooplankton that have allowed them to be so successful over time.

Plenary talk on gelatinous zooplankton by Larry Madin (Woods Hole Oceanographic Institute, U.S.A.).



At the Award Presentation Ceremony (from left to right): Christopher Mooney (Best Student Oral Presentation Award), Dr. Shin-ichi Uye, a grandmother of jellyfish study, Dr. Mary Arai (Lifetime Achievement Award), and Zhilu Fu (Best Student Poster Presentation Award).

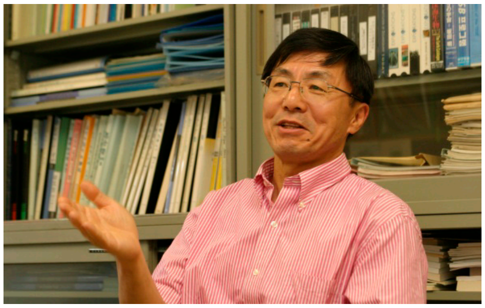
The symposium also consisted of nine sessions dealing with such diverse topics as physiology, production, growth, reproduction, and feeding dynamics (http://home.hiroshima-u.ac.jp/ijfs/program.html). It culminated in a series of presentations highlighting the impacts that jellyfish blooms have on human enterprises including not only the negative aspects of preying on or competing with fish of ecological or commercial importance, but also stressing their beneficial aspects including their role in sequestering CO_2 to the deep ocean and provisioning of food resources to humans, especially within many PICES member countries.

In addition to the scientific accomplishment of the symposium, the participants were able to enjoy the many local Japanese cultural and culinary delights of the Hiroshima region, including a post-meeting excursion to Miyajima, a World Heritage site located nearby.

The Award Presentation Ceremony took place during the symposium reception which followed the field trip. A Lifetime Achievement Award was presented to Dr. Mary Arai (Department of Fisheries and Oceans, Canada; retired) for her outstanding contributions to the taxonomic and ecological body of knowledge available for the gelatinous taxa. Two Best Student Presentation Awards were given to Christopher Mooney (James Cook University, Australia) for his talk on "Experimental calibration of elemental incorporation into *Chironex fleckeri* statoliths resulting from changes in salinity" and to Zhilu Fu (Hiroshima University, Japan) for her poster on "Point-of-no-return in ephyrae of the moon jellyfish *Aurelia aurita*".

The meeting was a complete success and the participants are already looking forward to the 5th International Jellyfish Bloom Symposium slated to be held in 2016, in Barcelona, Spain.

The symposium elevated the status of the PICES WG 26 worldwide. The Working Group also held a 1-day inter-sessional meeting in advance of the symposium (on June 4) to take advantage of the expertise coming to the meeting, to present reports on new topics and achievements in jellyfish bloom research in PICES member countries, and also move forward on the WG 26 final report. The draft of this report is expected to be completed by the end of this year.



Dr. Shin-ichi Uye (suye@hiroshima-u.ac.jp) is a Professor of biological oceanography at Hiroshima University. Shin-ichi is currently involved in two Japanese jellyfish research projects: Studies on Prediction and Control of Jellyfish Outbreak (STOPJELLY) and the China-Japan-Korea International Project on the Giant Jellyfish Bloom. He was former President of the Plankton Society of Japan (2001–2004) and former President of the World Association of Copepodologists (2005–2008). Shin-ichi was awarded the Oceanographic Society of Japan Prize in 2010 for his advancement of zooplankton research, particularly on their functional roles in coastal marine ecosystems. Shin-ichi now serves as a Co-Chairman of the PICES Working Group on Jellyfish Blooms around the North Pacific Rim: Causes and Consequence.

Dr. Richard Brodeur (Rick.Brodeur@noaa.gov) is a Research Fisheries Oceanographer working in the Fish Ecology Division of the Northwest Fisheries Science Center, NOAA Fisheries, and is based in Newport (Oregon, U.S.A.). Ric began his career working on early life history and recruitment dynamics of walleye pollock in the Gulf of Alaska and Bering Sea for the Alaska Fisheries Science Center and became interested in jellyfish following their dramatic increase in that ecosystem. He has published on a variety of topics ranging from satellite oceanography to fish bioenergetics to fisheries acoustics, but has focused much of his research on feeding and food web interactions in the pelagic ecosystem. Ric has been heavily involved in PICES, serving on several committees and expert groups and organizing a number of special sessions and workshops at past meetings. He serves now as a Co-Chairman of the PICES Working Group on Jellyfish Blooms around the North Pacific Rim: Causes and Consequence.