PICES XIII S5-1777 Oral
Anthropogenic invasion of some benthic species in the coastal areas

Tatyana A. **Belan**

Far Eastern Regional Hydrometeorological Research Institute, 24 Fontannaya Street, Vladivostok, 690990, Russia
E-mail: tbelan@hydromet.com

Negative environmental impacts caused by introduced exotic species are considered as problematic for coastal ecosystems. Since the 1980s the ctenophore *Mnemiopsis leidyi* has invaded the Azov and Black Seas. Further, species native to Japan, appeared along southeastern Australia (starfish *Asterias amurensis*), in San Francisco Bay (clam *Potamocorbula amurensis*) and in Atlantic coastal waters (shore crab *Hemigrapsus sanguineus*).

Other problems are caused by the invasion of small local opportunistic species is their spread and the replacement of common benthic organisms. Since the 1970s and 1980s some species (considered to be rare in the middle of the last Century) were spreading and are abundant today in urban and industrial regions of different geographical zones. Polychaetes of the Genus *Schistomeringos* became dominant in coastal waters of the Black Sea, Japanese Sea and NE Pacific (Losovskaya, 1977; Kiseleva *et al.*, 1984; Levings, 1985; Burd *et al.*, 1990; Bagaveeva, 1992). In some Black Sea bays the polychaete *Polydora limicola* became widespread with a high density since 1970s. In the middle of 1980s, the polychaete *Tharyx pacifica* was dominant in coastal urban regions of the Japanese Sea. From the 1940s to 1960s these species were not observed or occurred in very low numbers.

As a rule, the highest abundance of these species was recorded in ecologically stressed areas with high concentrations of contaminants, low dissolved oxygen content and where other anthropogenic impacts are registered. One of the reasons for the wide distribution of these species is their ecological flexibility and persistence under different kinds of environmental disturbances.

PICES XIII S5-2036 Oral
Is mid-ocean exchange effective in preventing the invasion of estuaries by zooplankton from ships' ballast water?

Jena M. **Bills**, G. Smith, K.H. Choi, W.J. Kimmerer and G.M. Ruiz

Romberg Tiburon Center for Environmental Studies, 3152 Paradise Drive, Tiburon, CA, 94920, U.S.A. E-mail: earthmuffinj@yahoo.com

The number of non-indigenous invasive species (NIS) in North American estuaries has dramatically increased over the last century. Ships' ballast water has been identified as one of the major vectors of transport of NIS between estuaries worldwide. Various ballast water management strategies have been suggested to reduce the likelihood of high-impact invasions such as the zebra mussel. Mid-ocean exchange of ballast is relatively inexpensive, and is the only management strategy currently being applied routinely to reduce the influx of NIS. Surveys of ballast water entering North American ports suggest that exchange does not remove all estuarine organisms. We conducted experiments aboard container ships to assess the efficacy of mid-ocean ballast exchange for the removal of estuarine zooplankton. Samples were collected from paired tanks at the beginning and end of eight voyages of container ships, in which one tank underwent an exchange and the other was left unexchanged (as a control). The tracer dye used in these studies showed that mid-ocean exchange removed 75-98% of the original ballast water. The removal rate of estuarine zooplankton was, on average, proportional to the removal of rhodamine dye. Exchange efficiency however, varied as a function of the population dynamics in the control tanks. These results could help us to understand how efficient mid-ocean exchange is and whether it is an acceptable means of eradicating potential invaders from ballast water.

PICES XIII S5-2094 Oral

Ballast water exchange verification using the optical characteristics of dissolved organic matter

Jennifer **Boehme**[1] and Mark Wells[2]

[1] Darling Marine Center, University of Maine, 193 Clarks Cove Road, Walpole, ME, 04573, U.S.A. E-mail: jboehme@maine.edu
[2] University of Maine, School of Marine Sciences, 201 Libby Hall, Orono, ME, 04469, U.S.A.

The release of ballast water carried by international shipping traffic into freshwater and marine ports has previously resulted in ecosystem devastation and substantial economic costs from the invasion and establishment of exotic species transported within ballast tanks. The International Maritime Organization established voluntary guidelines in 1991 employing mid-ocean ballast water exchange (BWE) to minimize ballast-mediated species invasions. The U.S. Coast Guard currently recognizes BWE as the only accepted method to control the spread of exotic species, and soon mandatory ballast exchange will be required and monitored for ships entering U.S. ports from outside the exclusive economic zone. Given that BWE will remain the leading method of invasive species control for at least the next decade, there is critical need to establish reliable and practical verification methods. Current monitoring methods employ salinity measurements as benchmarks for different water masses, but its usefulness as a tracer is not universal.

The optical character and intensity of colored dissolved organic matter (CDOM) has been explored as a more sophisticated tracer for the origin of ballast water. CDOM is strongly influenced by biotic and abiotic input and removal processes tied to ecosystem structure and terrestrial forcing. Results from preliminary surveys of nearshore and offshore CDOM optical properties shows there are distinct features in these disparate environments that become readily discernable statistically. We build from these data to propose a novel but practical ecosystem-based approach for developing the instrumentation and associated database needed to achieve the projected verification requirements of the U.S. Coast Guard.

PICES XIII S5-2163 Oral

Onboard ballast water treatment using the Special Pipe to terminate aquatic organisms

Yasuwo **Fukuyo**[1], Takeaki Kikuchi[2], Katsumi Yoshida[2] and Seiji Kino[2]

[1] Asian Natural Environmental Science Center, the University of Tokyo, Yayoi 1-1-1, Bunkyo-ku, Tokyo, 113-8657, Japan
E-mail: ufukuyo@mail.ecc.u-tokyo.ac.jp
[2] The Japan Association of Marine Safety

The special pipe system was designed to terminate aquatic organisms in ballast water during water uptake and/or discharge, using shear stress and cavitation produced by special plate structures of the system. At land-based tests the termination efficacy, which was judged by the change in organisms' appearance, was 91.4% for phytoplankton and 99.9% for zooplankton at a one-time passage through the pipe. A two-time passage resulted in an phytoplankton inactivation of 99.4% and 100% for zooplankton. The results showed also that higher flow rates and multiple passages had a higher efficacy.

Further tests were conducted onboard a container vessel of 53,822 gross tonnage equipped with 33 ballast tanks with a total ballast capacity of 21,219.9 tonnes. The vessel routinely cruises along China, Japan, U.S.A., Canada, Japan and China in a round-trip of 35 days duration. Data of organisms and environmental parameters were collected during two round-trips in November 2003 and February 2004. The treatment efficacy of the organisms was calculated according to the ballast water discharge quality standard of the IMO Ballast Water Management Convention: (1) organisms of 10-50 µm in minimum dimension could be reduced to meet the IMO standard (<10 ind./ml), (2) organisms larger than 50 µm could be reduced in some cases, but not in the others to meet the IMO requirement (<10 ind./m^3), (3) in some coastal areas more than 100,000 ind./m^3 larger than >50 µm were found. 4) *Vibrio cholerae* was not detected. *Escherichia coli* was found 1-3 cfu/100 ml at Los Angeles, Seattle and Vancouver.

PICES XIII S5-2178 Oral

The Ballast Water convention and its inherent, but inevitable incompleteness for the prevention of biological invasion

Yasuwo **Fukuyo**

Asian Natural Environmental Science Center, the University of Tokyo, Yayoi 1-1-1, Bunkyo-ku, Tokyo, 113-8657, Japan
E-mail: ufukuyo@mail.ecc.u-tokyo.ac.jp

The International Convention for the Control and Management of Ships' Ballast Water and Sediments was adopted at a Diplomatic Conference at the International Maritime Organization in February 2004. This convention aims to prevent and ultimately eliminate risks to the environment, human health, property and resources arising from the transfer of harmful aquatic organisms and pathogens through the control and management of ships' ballast water and sediments. It looks like aiming to terminate harmful species only, but the real target is all organisms taken in tanks together with ballast water, because all organisms in tanks will be discharged at ports, and potentially settle and proliferate. Proliferated groups of organisms occupy a certain ecosystem niche and eventually change the environment, regardless of direct harmfulness to human and natural resources.

The maximum allowable number of organisms in water to be discharged at ports is defined as follows; 1) viable organism of the size larger than or equal to 50 µm in its minimum dimension shall be less than 10 individuals in one cubic meter, 2) viable organisms smaller than 50 µm and larger than or equal to 10 µm in the minimum dimension shall be less than 10 individuals in one milliliter, 3) three indicator pathogenic bacteria. These criteria are challenging not only to the maritime industry, but also to marine science. Because the first criterion mentioned above is difficult to achieve by the industry and also difficult to prove or confirm by scientists at approval experiments. The second criterion is too lax to prevent invasion of organisms.

PICES XIII S5-1901 Oral

Marine invasive species transported by vessel hull fouling: Potential management approaches

L. Scott **Godwin**

B.P Bishop Museum, Natural Sciences Department, Hawaii Biological Survey, 1525 Bernice Street, Honolulu, HI, 96817-2704, U.S.A.
E-mail: sgodwin@bishopmuseum.org

Ocean-going vessels can be thought of as biological islands for species that dwell in harbors and estuaries around the world. Maritime vessel activity acting as a vector for marine alien species is a complex issue involving ballast water, ballast water sediments, and hull fouling. Ballast water is the pathway that has been the major focus of investigations concerned with marine invasion vectors, and the biofouling that occurs on the surfaces of vessel hulls has been given less attention. Recent compilations of marine alien species in Hawaii include some 343 species, which includes 287 marine invertebrate species. The mechanism of transport for more than 70% of these marine invertebrate species is considered to be hull fouling. Pending administrative rules focused on management efforts for ballast water have recently moved toward mandatory exchange for all United States ports. Hull fouling is a new management issue, and will require expert opinions from various stakeholders connected to maritime shipping, marine resource management, and marine alien species problems. Such an effort was recently undertaken in Hawaii and the goal was to develop initial ideas that could be used to develop a formal management strategy. It was shown that it could be more important to focus management efforts on stochastic events instead of regular arrivals to minimize marine invasive species introductions through hull fouling.

PICES XIII S5-1969 Invited
Ballast water – The key vector for aquatic species invasions?

Stephan **Gollasch**

GoConsult, Bahrenfelder Str. 73a, Hamburg, 22765, Germany. E-mail: sgollasch@aol.com

The major vectors for unintentional species introductions in aquatic habitats are shipping and species introductions for aquaculture. Inventories of aquatic invaders in many regions have shown that shipping is the predominant vector of species invasions. Historically hull fouling was the most important introducing vector. Nowadays, ballast water becomes more into focus. The global merchant fleet of more than 40,000 vessels discharges approx. 3 billion tonnes of ballast water annually. It is estimated that more than 4,000 species are in transit with ships in high individual numbers at any one time. As a result each single vessel carries an enormous number of organisms and therefore all coastal regions receiving ballast water discharges are at high risk of new species introductions. This account compares the relative importance of vectors for species introductions with an emphasis on shipping.

PICES XIII S5-2191 Oral
ICES and biological invasions - introduction to the work of ICES Working Group on Introductions and Transfers of Marine Organisms and ICES/IOC/IMO Working Group on Ballast and Other Ship Vectors

Stephan **Gollasch**

GoConsult, Bahrenfelder Str. 73a, Hamburg, 22765, Germany. E-mail: sgollasch@aol.com

As a fishery-oriented inter-governmental organisation, ICES has been confronted early on with issues related to the introductions of non-indigenous species, in particular diseases and parasites transferred with live transport of fish and shellfish for relaying, stocking, ranching and for immediate human consumption. During the early 1970s, decisions on recommendations regarding introductions and transfers were mainly discussed in the ICES Consultative Committee. Consequently the ICES Working Group on Introductions and Transfers of Marine Organisms (WGITMO) was launched at held the first meeting as reconvening working group in 1979. The 25th meeting was held in 2003. In the beginning the group dealt with intentional introductions only. In the beginning 1990s unintentional, ship-mediated introductions came more into focus and WGITMO suggested to establish a new stand-alone working group to focus on ships as transport vector. The Study Group on Ballast Water and Sediments (ICES/IOC/IMO SGBWS) was established by ICES Council Resolution in 1996. To address the growing concern of other shipping vectors the Study Group was renamed to Study Group on Ballast and Other Ship Vectors (ICES/IOC/IMO SGBOSV) in 1999. In 2003 the status of this group was changed and the group was re-established as the Working Group on Ballast and Other Ship Vectors (ICES/IOC/IMO WGBOSV). Both groups substantially contributed to various ICES publications, including the ICES Code of Practice on Introductions and Transfers of Non-indigenous Marine Organisms (most recent version published in 2003), Alien Species Alert Reports, Status Report of Introductions of Non-Indigenous Marine Species into North-Atlantic Waters 1981-1991 published as ICES Cooperational Research Report (the 1992-2002 version is in preparation). Comprehensive meeting reports of both groups are available at the ICES homepage www.ices.dk.

PICES XIII S5-2022 Invited
Range extensions and ship ballast water transport of harmful algal bloom species in the Australian region

Gustaaf M. **Hallegraeff**

School of Plant Science, University of Tasmania, Private Bag 55, Hobart, Tasmania, 7001, Australia. E-mail: Hallegraeff@utas.edu.au

The role of ship's ballast water in the spreading of harmful marine microalgae is examined, with a focus on diatoms and dinoflagellates which can impact human health, fisheries, aquaculture and the environment. In extensive Australian ship ballast water surveys, 80% of ships contained culturable diatom species (including potentially toxic

Pseudo-nitzschia, causative organisms of Amnesic Shellfish Poisoning) and 5% of ships contained the Paralytic Shellfish Poisoning producing dinoflagellates *Alexandrium catenella, A. tamarense* and *Gymnodinium catenatum* (up to 300 million viable cysts in a single ship). The potentially ichthyotoxic dinoflagellate *Pfiesteria piscicida* has also been cultured from ballast water entering Australian ports. While the presence of harmful marine microalgae in ballast water thus has been firmly established, to prove that a particular species of microorganism has been introduced is complex and relies on the study of dinoflagellate cysts in dated sediment cores (*Gymnodinium catenatum* in Tasmania) and increasingly the application of sophisticated molecular sequencing. To reduce the risk of ballast water introductions by these microorganisms (mostly 10 to 100 m size) represents a very significant scientific and technological challenge, which cannot yet be adequately achieved with best currently available technologies (*e.g.* 95% ballast water exchange). Examples of promising but expensive higher standard treatment technologies include heating, mechanical removal of organisms in combination with UV treatment, as well as chemical treatment of ballast water. By contrast, we have no control over range extensions resulting from *e.g.* climate induced shifts in ocean conditions. Increasing red tide blooms by the dinoflagellate *Noctiluca scintillans* in Tasmanian waters (2001-2004) thus are thought to represent a recent East Australian Current driven range extension from Sydney coastal waters into Tasmanian waters, where it now has established permanent overwintering populations.

PICES XIII S5-2135 Oral
Range expansion and speed of spread by introduced marine benthos in Japan

Keiji **Iwasaki**[1] and The Committee for the Preservation of the Natural Environment, The Japanese Association of Benthology

[1] Institute for Natural Science, Nara University, 1500 Misasagi-cho, Nara, 631-8502, Japan. E-mail: iwasaki@daibutsu.nara-u.ac.jp

To investigate the invasion history and current geographic distribution of marine benthos introduced to Japan, the Committee for the Preservation of the Natural Environment, the Japanese Association of Benthology, conducted a questionnaire survey on their occurrence in the field, including both published and unpublished records in 2002-2003. In total 88 taxa were reported by 94 respondents. Taxa were categorized according to three criteria (1) known or unknown geographic origin, (2) established invasion history and (3) presumed dispersal mechanisms associated with human activities. As a result 42 taxa were designated as non-indigenous species introduced to Japan through human activities, 26 taxa as indigenous species which are known from Japan and other countries but are introduced from abroad to Japan for fisheries or as fish bait, and 20 cryptogenic taxa. The analysis of the first record years of the 42 non-indigenous species revealed that the invasion rate has increased over the past century, with seven or eight species being introduced per decade after 1960. Data on the temporal distributional change revealed that many non-indigenous species have become widespread recently, from the Pacific coasts of central Japan to the coasts of the Sea of Japan or northwards. Their rate of spread was calculated through the regression analyses of (a) the distance between the area of first record and the most distant site of known occurrence and (b) against the time after the year of first record. The calculation resulted in a rate of spread ranging from 10 – 26 km year^{-1}. In unintentionally introduced species the first record site was considered as starting point for the dispersal in Japan.

PICES XIII S5-1795 Oral
Small craft as a vector of exotic species

Dan **Minchin**[1], Anna Occhipinti[2], Oliver Floerl[3] and Dario Savini[2]

[1] Marine Organism Investigations, 3 Marina Village, Ballina, Killaloe, Co Clare, IRL, Ireland. E-mail: minchin@indigo.ie
[2] Department of Genetics and Microbiology, University of Pavia, Via S. Epifanio, 14, 27100 Pavia, Italy
[3] National Institute of Water and Atmospheric Research, PO Box 8602, Christchurch, New Zealand

Small craft are potential vectors for the distribution of aquatic organisms in freshwater, brackish and marine environments. Such craft vary in design from small open boats, yachts and cruisers to small working vessels. Fouling of biota on hull surfaces, engine components, abstraction ports, tunnels and projections result in varying numbers of non-indigenous species being transported but it is possible that contained water could also result in transmissions. In this account we demonstrate that the number of small craft continue to increase in temperate,

Mediterranean and semi-tropical environments and that the spread of some exotic species by small craft to local and distant regions can take place. Some vessels such as yachts can range widely and may be capable of transmissions across oceans. However, movements of yachts tend to be limited according to the availability of favourable trade winds and avoidance of areas during months when tropical storms occur. Marina sites in port regions are considered to be vulnerable areas should shipping result in exotic species introductions.

PICES XIII S5-1775 Poster

Ichthyofaunal exchange between northwestern and northeastern Pacific: Possible directions and mechanisms

Alexei M. **Orlov**

Russian Federal Research Institute of Fisheries & Oceanography, 17, V. Krasnoselskaya, Moscow, 107140, Russia
E-mail: orlov@vniro.ru

Until today only the continental slope of the Bering Sea is considered as migration pathway for pelagic eggs/larvae of American ichthyofauna to Asian coasts (Pacific halibut *Hipposlossus stenolepis*, sablefish *Anoplopoma fimbria*, shortraker rockfish *Sebastes borealis*, arrowtooth flounder *Atheresthes stomias*, rex sole *Glyptocephalus zachirus*). Recent studies showed that an exchange of Asian and American ichthyofaunas occurs along the Kuril and Aleutian Islands. Some species significantly extended their ranges westwards from the Aleutian to Kuril Islands and southeastern Kamchatka due to recent climatic changes (northern rockfish *Sebastes polyspinis*, light dusky rockfish *Sebastes ciliatus*, arrowtooth flounder, and rex sole). Some species described from the Aleutian Islands (blacktip snailfish *Careproctus zachirus*, longfin Irish lord *Hemilepidotus zapus*, scaled sculpin *Archaulus biseriatus*, sponge sculpin *Thyriscus anoplus*, and roughskin sculpin *Rastrinus scutiger*) were recently found abundant or common in Pacific waters off the Kuril Islands. Off the Aleutian Islands the species listed above are very rare (and mostly small-size immature specimens are found) while off the Kuril Islands the adults are very common. It is suggested that pelagic eggs or larvae of these species may be transported from Kuril Islands to the Aleutians by the Western Pacific Gyre.

PICES XIII S5-2157 Oral

Effect of UV radiation exposure on marine microplankton: Results of a mesocosm study simulating ballast water treatment

Gretchen **Rollwagen-Bollens**[1,2], Stephen M. Bollens[1,2], Jeffery R. Cordell[3]and Anne M. Slaughter[1]

[1] Department of Biology and Romberg Tiburon Center for Environmental, Studies, San Francisco State University, 3152 Paradise Drive, Tiburon, CA, 94920, U.S.A. E-mail: rollboll@sfsu.edu
[2] School of Biological Sciences, Washington State University Vancouver, 14204, Salmon Creek Ave., Vancouver, WA, 98686, U.S.A.
[3] School of Aquatic and Fishery Sciences, University of Washington, P.O. Box, 355020, Seattle, WA, 98195-5030, U.S.A.

Introduction of non-indigenous species in aquatic ecosystems is a growing area of research, as evidence of negative effects of non-indigenous taxa has increased in recent years. For example, several copepod species have been introduced into NE Pacific estuaries, with some showing significant impacts on the ecology of the invaded systems (*e.g.* Tortanus dextrilobatus has become a major predator on smaller native copepods in the San Francisco Estuary). With the realization of important ecological impacts of invasive species has come the desire to find treatment and/or mitigation approaches to reduce or eliminate the effects of these introductions. One approach is to treat ballast water with UV radiation in an attempt to eradicate planktonic organisms before they are released into new environments. In order to evaluate the feasibility of such an approach, we undertook well-replicated and controlled mesocosm experiments over a three-week period, to examine the effects of UV radiation on micro- and mesozooplankton from Puget Sound, WA, USA. UV exposure of 60-200 mJ proved effective in reducing overall microplankton abundance relative to controls, but did not effect chl a concentrations. Moreover, the microplankton community composition changed substantially, with free-living dinoflagellates (*e.g.* Protoperidinium) eventually replaced by aloricate ciliates (*e.g.* Euplotes, Uronema) and several types of (presumably) dinoflagellate cysts. These experiments demonstrate the potential utility of UV treatment to reduce plankton abundance, however the observed compositional changes and cyst formation remain important issues to be addressed if this treatment approach is to be implemented.

PICES XIII S5-2139 Oral
Introduced seaweeds – Genetic diversity of introduced and native *Undaria pinnatifida*

Shinya **Uwai**[1], Wendy Nelson[2], Luis E. Aguilar-Rosas[3], Sung Min Boo[4] and Hiroshi Kawai[1]

[1] Kobe University Research Center for Inland Seas, Kobe University, Rokkodai 1-1, Nadaku, Kobe, Hyogo, 657-8501, Japan
E-mail: uwai@kobe-u.ac.jp
[2] National Centre for Aquatic Biodiversity and Biosecurity, NIWA, Private Bag 14-901, Wellington, New Zealand
[3] Instituto de Investigaciones Oceanológicas Universidad Autónoma de Baja California, Km. 103 carretera Tijuana-Ensenada, 22830, México
[4] Department of Biology, Chungnam National University, Daejon, 305-764, Republic of Korea

More than 100 seaweeds are considered to have expanded their geographic range supported by human activities, and are called “introduced seaweeds”. Some of them are known to have proliferated vigorously and show hazardous impacts to coastal ecosystems of the recipient site (*e.g. Sargassum muticum, Undaria pinnatifida* and *Caulerpa taxifolia*). The native area of *U. pinnatifida* is the coastal Northwestern Pacific (Japan, Korea and eastern China). However, this species is now introduced to Europe, Pacific North America (California to Mexico), southeastern Australia, New Zealand, and Argentina. Seed populations are believed to be transported with oysters for mariculture in Europe, and by ballast water in Oceania, although actual vectors and secondary spread pathways are not well understood. To elucidate the origin of American and southern hemisphere populations of *U. pinnatifida*, and to discuss the pathways of the secondary spread, we investigated the genetic diversities among the populations around the world using mitochondrial *COX3* DNA sequence. For the native area, *U. pinnatifida* populations of western Japan showed relatively high genetic diversity (six haplotypes), whereas, those of northeastern Japan showed only a single haplotype. This haplotype was also found from the mariculture strain and in some areas in western Japan where *Undaria* mariculture is ongoing. Introduced populations in Europe, America, and Oceania also share this haplotype, suggesting their origin from the Northern Japan (or mariculture) populations. However, New Zealand populations included a second haplotype, implying multiple introductory events for the New Zealand populations.

PICES XIII S5-1928 Invited
What do temporal trends in invasion records really mean?

Marjorie J. **Wonham**[1] and Elizaveta Pachepsky[2]

[1] Centre for Mathematical Biology, University of Alberta, Edmonton, AB, T6G 2G1, Canada. E-mail: mwonham@math.ualberta.ca
[2] Ecology Evolution & Marine Biology, University of California Santa Barbara, Santa Barbara, CA, 93106-9610, U.S.A.
E-mail: pachepsk@lifesci.ucsb.edu

Biological invasions in many marine systems appear to be increasing and perhaps even accelerating, but these trends are notoriously difficult to interpret. Hypotheses to account for the apparent increase in invasions include an increase in introduction rates, invasion success, and reporting. Distinguishing among these hypotheses requires a clear distinction among their null expectations. To this end, we introduce a simple probabilistic framework for considering the number of successful invaders over time as a function of introduction rates and survival probabilities, and compare the model's predictions to empirical data. We show that empirical data are best analysed as a non-cumulative distribution of introduction times, that an increasing distribution of introduction times does not necessarily indicate an increasing introduction rate or survival probability, and that simple variation in introduction rates and survival probabilities can generate apparently linear, quadratic, exponential, or sigmoid distributions of introduction times.