

Frontiers in Ecology and the Environment

Is global ocean sprawl a cause of jellyfish blooms?

Carlos M Duarte, Kylie A Pitt, Cathy H Lucas, Jennifer E Purcell, Shin-ichi Uye, Kelly Robinson, Lucas Brotz, Mary Beth Decker, Kelly R Sutherland, Alenka Malej, Laurence Madin, Hermes Mianzan, Josep-Maria Gili, Verónica Fuentes, Dacha Atienza, Francesc Pagés, Denise Breitburg, Jennafer Malek, William M Graham, and Robert H Condon

Front Ecol Environ 2012; doi:10.1890/110246

This article is citable (as shown above) and is released from embargo once it is posted to the *Frontiers* e-View site (www.frontiersinecology.org).

Please note: This article was downloaded from *Frontiers e-View*, a service that publishes fully edited and formatted manuscripts before they appear in print in *Frontiers in Ecology and the Environment*. Readers are strongly advised to check the final print version in case any changes have been made.



Is global ocean sprawl a cause of jellyfish blooms?

Carlos M Duarte^{1*,2}, Kylie A Pitt³, Cathy H Lucas⁴, Jennifer E Purcell⁵, Shin-ichi Uye⁶, Kelly Robinson⁷, Lucas Brotz⁸, Mary Beth Decker⁹, Kelly R Sutherland¹⁰, Alenka Malej¹¹, Laurence Madin¹², Hermes Mianzan¹³, Josep-Maria Gili¹⁴, Verónica Fuentes¹⁴, Dacha Atienza¹⁴, Francesc Pagés^{1†}, Denise Breitburg¹⁵, Jennafer Malek¹⁵, William M Graham¹⁶, and Robert H Condon⁷

Jellyfish (Cnidaria, Scyphozoa) blooms appear to be increasing in both intensity and frequency in many coastal areas worldwide, due to multiple hypothesized anthropogenic stressors. Here, we propose that the proliferation of artificial structures – associated with (1) the exponential growth in shipping, aquaculture, and other coastal industries, and (2) coastal protection (collectively, “ocean sprawl”) – provides habitat for jellyfish polyps and may be an important driver of the global increase in jellyfish blooms. However, the habitat of the benthic polyps that commonly result in coastal jellyfish blooms has remained elusive, limiting our understanding of the drivers of these blooms. Support for the hypothesized role of ocean sprawl in promoting jellyfish blooms is provided by observations and experimental evidence demonstrating that jellyfish larvae settle in large numbers on artificial structures in coastal waters and develop into dense concentrations of jellyfish-producing polyps.

Front Ecol Environ 2012; doi:10.1890/110246

Multiple explanations have been suggested for possible drivers of the apparent increase of jellyfish blooms in many coastal waters around the globe, including the depletion of predators and competitors of jellyfish by overfishing, accidental translocations, eutrophication of coastal waters, changes in freshwater flows, human modification of coastal geomorphology, and climate change (Mills 2001; Purcell *et al.* 2007; Purcell 2012). Most of these explanations focus on factors that affect the performance of the pelagic phase of jellyfish; however,

the life history of many jellyfish species includes an often unnoticed benthic stage – in the form of polyps – from which jellyfish are produced (Boero *et al.* 2008). A major obstacle in identifying the causes underlying these jellyfish blooms lies in the difficulty of locating the habitat of the polyps from which the most problematic coastal jellyfish blooms develop (Mills 2001; Boero *et al.* 2008). In most coastal jellyfish species with bipartite life histories, embryos develop into free-swimming planula larvae, which settle on hard substrates and metamorphose into sessile polyps (Boero *et al.* 2008). These polyps eventually develop into juvenile medusae, such as in box jellyfish or cubozoans, or segment asexually (ie strobilate) to release juveniles named ephyrae, as is the case in the true jellyfish or scyphozoans (Arai 1997). Jellyfish polyps are very small (a few millimeters in length; Figure 1), are inconspicuous, and typically inhabit shaded environments, often suspended underneath horizontal surfaces of rocks and shells (Pitt 2000; Holst and Jarms 2007). The small size of the polyps and the difficulty of sampling them complicates locating and measuring polyp colonies in the vast coastal, marine, and estuarine environments.

Here, we examine the hypothesis that the growing proliferation of artificial structures associated with shipping, aquaculture, and other coastal industries, as well as the number and size of shoreline stabilizing structures, provides habitat for jellyfish polyps; such structures may therefore play an important role in increasing the numbers of jellyfish blooms. Support for this hypothesis is derived from observations and experimental evidence demonstrating that jellyfish larvae settle in abundance on artificial structures in coastal waters, forming dense concentrations of polyps.

In a nutshell:

- Increases in jellyfish blooms have been reported across coastal locations worldwide
- Explanations for this phenomenon have focused on factors that enhance the performance of swimming jellyfish, but the importance of the benthic polyp stage, which produces the bloom-forming jellyfish, has been largely overlooked
- The increase of jellyfish polyp habitat associated with the proliferation of artificial structures in coastal zones is examined as a driver of jellyfish blooms
- Reports of jellyfish polyps on artificial substrates and experiments showing their preference for these substrates provide supporting evidence

¹The Oceans Institute, University of Western Australia, Crawley, Australia (*carlos.duarte@uwa.edu.au); ²Department of Global Change Research, Instituto Mediterráneo de Estudios Avanzados, Esporles, Spain; ³Australian Rivers Institute and Griffith School of Environment, Griffith University, Gold Coast, Australia; ⁴School of Ocean & Earth Science, University of Southampton, National Oceanography Centre, Southampton, UK; (continued on last page)

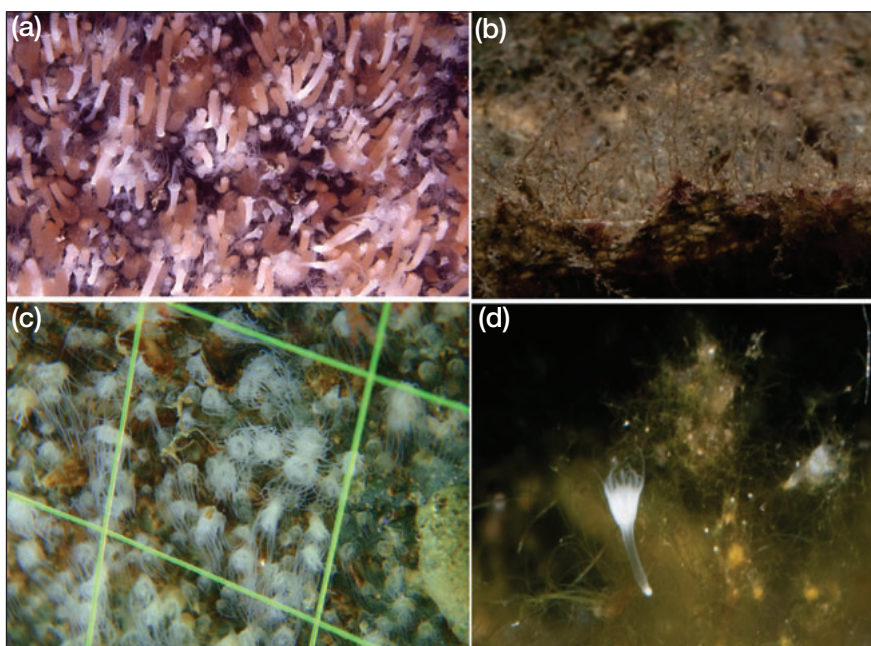


Figure 1. Photographs of jellyfish polyps attached to artificial structures. (a) Strobilating polyps of *Aurelia labiata* attached to a marina float in Cornet Bay, Washington State (5 cm × 7 cm; from Purcell et al. 2009); (b) hydroids of *Obelia dichotoma* attached to plastic debris in the Ebro Delta, Spanish Mediterranean; (c) polyps of *A. aurita* attached to a floating pier in the Inland Sea of Japan (2.3 cm × 3 cm); and (d) polyp of *Cotylorhiza tuberculata* attached to sunken piers in abandoned aquaculture concessions in the Mar Menor, Spanish Mediterranean.

Polyps were generally located by both visual and photographic surveys, carried out by divers (Table 1; Figure 1). Where species identification was not possible for the polyp stage, the polyp aggregations were collected and reared in the laboratory until liberated ephyrae grew to young medusae that could be readily identified.

Two experiments – one involving *Chrysaora quinquecirrha* in Chesapeake Bay and the other consisting of *Cotylorhiza tuberculata* in the Mediterranean Sea – were conducted to assess the settlement preferences of jellyfish planulae. The Chesapeake Bay experiments with *C. quinquecirrha* were conducted during summer 2010, in Mackall Cove (St Leonard, Maryland), a sub-estuary of Chesapeake Bay where *C. quinquecirrha* is abundant. This experiment was designed to assess larval settlement onto oyster shells, flagstones, aged copper azole pressure-treated wood, and steel substrates, representing some of the potential natural and artificial substrates available in the Chesapeake. Recruitment panels (12.7

Observations of the presence of jellyfish polyps on artificial substrates were derived from surveys conducted by the authors across many locations and habitats, involving hundreds of SCUBA diving hours, and complemented by the earlier findings of others (Tables 1 and 2; WebPanel 1).

cm × 10.1 cm) were constructed by gluing the test substrates onto PVC plates that were deployed with the settlement surfaces facing downward. The panels were deployed for 39 days at approximately 0.5 m below the water's surface, in a randomized block design. Each experimental

Table 1. Survey observations of jellyfish polyps associated with artificial structures

| Species | Life form | Location | Structure |
|--------------------------------|--------------------|--|---|
| <i>Aurelia aurita</i> | Polyp | Inland Sea of Japan (Japan) | Underside of floating docks and buoys and on pier pylons |
| <i>A. aurita</i> | Polyp | Southampton Water (UK) | Undersides of floating pontoons |
| <i>A. aurita</i> | Polyp | Horsea Lake (UK) | Undersides of artificial reef structures placed on the lake bottom |
| <i>A. aurita</i> | Polyp | Mar Menor (Spain) | Polyeps attached to wood pilings of tourist docks; recurrent winter blooms of medusae |
| <i>Aurelia</i> sp | Polyp and ephyra | Koper harbor in the Gulf of Trieste, Adriatic Sea (Slovenia) | Underside of oyster shells attached to piers |
| <i>Cotylorhiza tuberculata</i> | Polyp | Mar Menor (Spain) | Polyeps attached to oyster shells and piers in abandoned aquaculture concessions; also inside plastic bottles found on the bottom; recurrent medusae blooms |
| <i>Obelia dichotoma</i> | Hydroid and medusa | Ebro Delta (Spain) | Fouling organisms on the plastic objects attached to the docks; medusae predominant in the plankton |

block contained one randomly ordered replicate of each substrate completely exposed to predators and a second replicate spaced approximately 2.5 cm from the first to exclude large predators that might be in crevices created by shoreline reinforcement structures. At the end of the experiment, the panels were placed in 7% acid Lugol solution, polyps were counted, and the total exposed surface area of each substrate was calculated by image analysis. We used a randomized block analysis of variance (ANOVA; PROC MIXED, SAS version 9.1) to test for effects of substrate type, exposure, and the substrate \times exposure interaction on the number of polyps per square centimeter on the panels. Data were rank transformed because of extreme heterogeneity of variances.

The laboratory experiment on settlement preferences of *C. tuberculata* planulae tested 16 types of substrates, both natural (sand, mud, shells, wood, rocks, plants) and artificial (bricks, ropes, cans, wood, concrete, plastic, glass). Each substrate had a surface area of 150 cm². Different substrates were placed with the settlement surfaces facing downward into 12-liter aquaria (three replicates) and planulae ($19\,250 \pm 1350$ [mean \pm standard error]) were added to each aquarium after one week. Parallel experiments were conducted in the presence and absence of light. Salinity (44–46 parts per thousand) and temperature (21–23.5°C) conditions maintained in the laboratory were similar to those in the Mar Menor lagoon (Murcia, Spanish Mediterranean), where the medusae were collected. Planulae were allowed to settle for 10 days; the resulting polyps were then counted in five areas of 10 cm² for each substrate type in each aquarium.

■ Presence of jellyfish polyps on artificial substrates

The surveys (Table 1) represent more than 2000 hours of diving over two decades in search of jellyfish polyps (data on surveys reported in WebPanel 1). Polyps were found across a range of artificial substrates off the coasts of Japan and the UK, as well as in the Mediterranean Sea (Table 1). The polyps were primarily located on the undersides of artificial structures in densities typically exceeding 10 000 individuals per square meter and up to 100 000 individuals per square meter, attached either directly to the artificial substrates or indirectly to oyster shells and tunicates on these substrates (WebPanel 1). Polyps were also observed as attached to vertical surfaces of artificial structures that had polyp colonies on the undersides, although densities were generally lower on the vertical surfaces than on the downward-facing surfaces. In some areas, years of surveys in

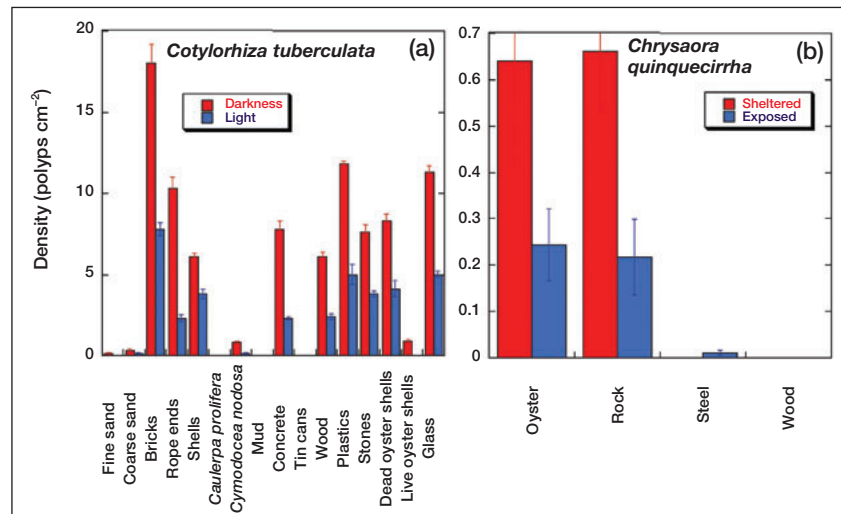


Figure 2. Experimental assessment of jellyfish planula settlement on different substrates for (a) *Cotylorhiza tuberculata* from the Mediterranean Sea and (b) *Chrysaora quinquecirrha* from Chesapeake Bay. Bars represent mean \pm standard error polyp density on different substrates and conditions (red and blue bars). Settlement differed significantly among substrates for both species (ANOVA, $P < 0.0001$; WebTable 1). Settlement of *C. tuberculata* was highly successful on hard substrates, particularly on smooth artificial surfaces including glass, plastic, or bricks, and in the dark (ANOVA, $P < 0.0001$; WebTable 1). Numbers of *C. quinquecirrha* polyps were similar on oyster shells, their natural habitat, and stones (t test, $P = 0.97$) and significantly higher (t test, $P < 0.005$) on recruitment panels spaced closely to exclude large predators as compared with more exposed panels.

search for polyps yielded no records of presence, but polyps were subsequently detected only when a new artificial structure was deployed in the surveyed area (WebPanel 1). Polyps were found in high densities on artificial substrates in harbors, suggesting they could be the site of massive potential releases of ephyrae (eg in excess of 1×10^{10} year⁻¹, calculated in the Port of Koper, Gulf of Trieste, Slovenia; WebPanel 1). Our surveys (Table 1) and accumulated published reports (Table 2) demonstrate the widespread use of artificial structures in coastal waters by species that produce jellyfish blooms. These species include both native and non-native jellyfish, such as native *Aurelia* spp, one of the most widespread blooming species of jellyfish, and the exotic invasive cubomedusa *Carybdea marsupialis* (Tables 1 and 2), the proliferation of which near tourist areas in the Mediterranean, where artificial structures abound, is of particular concern.

■ Experimental evidence of preference for artificial surfaces among jellyfish larvae

Experimental evidence that jellyfish larvae prefer to settle on artificial substrates has been reported for several jellyfish species (Holst and Jarms 2007; Hoover and Purcell 2009). Our experimental assessment of substrate preferences for settlement by *C. tuberculata* planulae in the Mediterranean and *C. quinquecirrha* planulae in Chesapeake Bay expands on these findings by revealing significant differences in settlement preferences across substrates (ANOVA,

Table 2. Summary of published reports of jellyfish life forms associated with artificial structures

| Species | Life form | Location | Structure | Reference |
|------------------------------------|----------------------|--|--|---|
| <i>Aurelia aurita</i> | Polyp | Coastal lagoon, Tapong Bay (Taiwan) | Polyps attached to oyster cultures | Lo <i>et al.</i> (2008) |
| <i>A. aurita</i> | Polyp | Wakasa Bay (Japan) | Underside of floating docks | Matsumura <i>et al.</i> (2005) |
| <i>A. aurita</i> | Polyp | Tokyo Bay (Japan) | On pylon in bottom hypoxic layer where other sessile organisms are absent | Ishii <i>et al.</i> (2008); Ishii and Katsukoshi (2010) |
| <i>A. aurita</i> | Polyp | Kagoshima Bay (Japan) | Underside of floating piers and buoys | Miyake <i>et al.</i> (2002) |
| <i>A. aurita</i> | Polyp | Murotsu fishing port, Yamaguchi (Japan) | Underside of floating piers; cellophane cover of cigarette packaging | Miyake <i>et al.</i> (2002) |
| <i>A. aurita</i> | Polyp | Conero Promontory, Ancona, Adriatic Sea (Italy) | Iron shipwreck | Di Camillo <i>et al.</i> (2009) |
| <i>A. aurita</i> | Polyp and ephyra | Bahía Blanca estuary (Argentina) | Maximum abundances close to harbors | Mianzan (1989) |
| <i>A. aurita</i> | Polyp | North Pacific coast (US) | Undersides of floating docks in marinas | Kozloff (1983) (cited in Purcell <i>et al.</i> 2009) |
| <i>A. labiata</i> | Polyp | Cornet Bay Marina, Washington (US) | Underside of marina floats | Purcell <i>et al.</i> (2009) |
| <i>Aurelia</i> spp | Polyp | Tasmania (Australia) | Undersides of breakwaters and floating docks | Willcox <i>et al.</i> (2008) |
| <i>Carybdea marsupialis</i> | Medusa | Denia, Valencia (Spain) | Newly released medusae only appear where breakwaters are installed | Bordehore <i>et al.</i> (2011) |
| <i>Chrysaora lactea</i> | Polyp and ephyra | Bahía Blanca estuary (Argentina) | Maximum abundances close to harbors | Mianzan (1989) |
| <i>Chrysaora quinquecirrha</i> | Medusa | Chesapeake Bay (US) | Wild and cultured oyster shells | Cargo and Schultz (1966) |
| <i>Cotylorhiza tuberculata</i> | Polyp | Ionian island of Lefkada (Greece) | Polyps attached to glass debris | Kikinger (1992) |
| <i>Cyanea capillata</i> | Polyp | Port Phillip Bay, Victoria (Australia) | Pier | Johnston and Keough (2000) |
| <i>Ectopleura larynx</i> | Hydroid and medusoid | Fish farms (Norway) | Predominant fouling organism collapsing fish-pen nets | Guenther <i>et al.</i> (2010) |
| <i>E. larynx</i> | Hydroid and medusoid | German Bight (Germany) | Offshore wind farm platform (fully covered 2 weeks after deployment) | Schroeder <i>et al.</i> (2006) |
| Filter feeders, including hydroids | Polyp | California (US) | Riprap | Pister (2009) |
| General "hydroids" | Polyp | Worldwide | Plastic floating debris | Barnes (2002) |
| <i>Obelia</i> spp; <i>Aurelia</i> | Hydroid and polyp | Puget Sound, Washington (US); also in San Francisco Bay (US) | Underside of floats; "sheets of <i>Aurelia scyphistoma</i> " in some locations | Kozloff (1983) (cited in Purcell <i>et al.</i> 2009) |
| <i>Rhizostoma pulmo</i> | Polyp and ephyra | Northeastern Spain | Polyps on concrete columns; ephyrae in plankton samples collected nearby | Fuentes <i>et al.</i> (2011) |

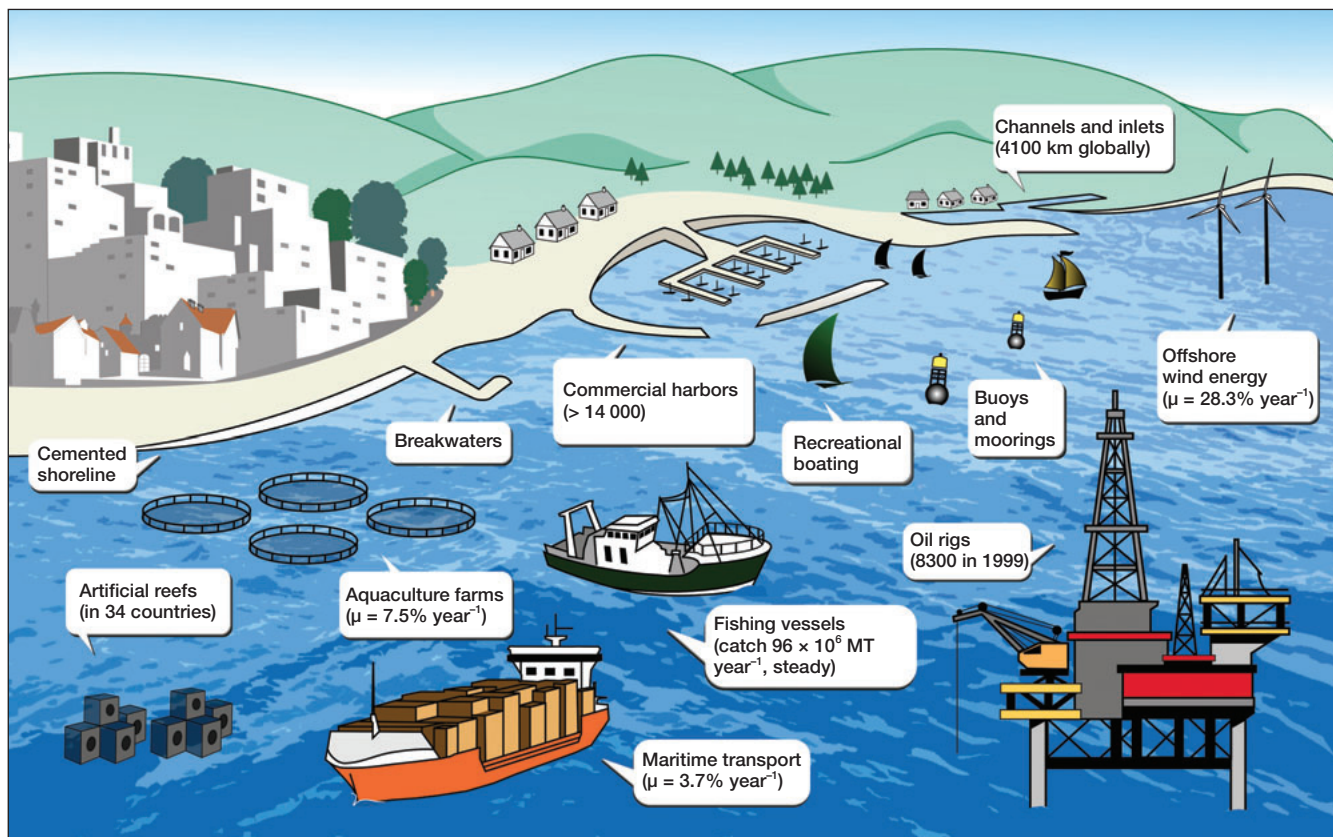


Figure 3. A representation of activities responsible for global ocean sprawl. Data sources – aquaculture production/growth and fisheries catch: FAO Fishstats (www.fao.org/fishery/statistics/software/fishstat); commercial harbors: the Ship Atlas (www.portinfo.co.uk); merchant fleet growth: Maritime Knowledge Center (www.imo.org/KnowledgeCentre, growth from 1990 to 2008); offshore wind energy: Global Wind Energy Outlook (www.gwec.net, growth expected from 2013 to 2020); length of channels and inlets: Waltham and Connolly (2011). MT = metric tons; μ = annual growth rate.

$P < 0.0001$; WebTable 1) and that recruitment of polyps on artificial substrates was comparable to or higher than that on natural substrates (Figure 2), particularly when the panels were spaced closely together, to exclude large predators, or else placed in the dark.

The evidence summarized here shows that jellyfish planulae preferentially settle on artificial substrates, which are often used as settlement plates to collect jellyfish polyps (Purcell *et al.* 2007). Consistent with these results, field surveys revealed the presence of jellyfish polyps on many artificial substrates. Potentially suitable artificial structures include submarine pillars, platforms and walls in harbors and piers, floating docks, oil rigs, aquaculture structures, platforms supporting coastal wind turbines, riprap, bridges, buoys, moorings, artificial urban waterways, ship hulls, artificial reefs, breakwaters, and garbage (Tables 1 and 2). The construction of artificial structures in coastal areas is growing at rates ranging from 3.7% year⁻¹ (merchant ships requiring harbor space) to 28.3% year⁻¹ (offshore wind energy), contributing to the increasing extent of global ocean sprawl (Figure 3).

The global ocean sprawl of artificial substrates suitable for jellyfish polyps is likely to be particularly critical in benthic regions with predominantly soft sediments (eg the Gulf of Mexico, the southeast coast of South America, and

the Yellow and East China seas), where natural hard substrates are scarce. Transport by hull fouling of ships or on oil platforms being located or relocated at sea provides mechanisms for invasive jellyfish translocations (Graham and Bayha 2007), with docks and harbor walls providing new dispersal centers for the invaders. The spatial arrangement of artificial structures may reduce distances between suitable settlement sites for larvae and thus act as “stepping stones” that facilitate range expansions and invasive processes, consequently increasing the spatial extent of blooms. The proliferation of these structures may compensate – or even overcompensate – for the disappearance of natural habitat, such as the decline in eastern oyster (*Crassostrea virginica*; Breitbart and Fulford 2006) abundance in Chesapeake Bay, the primary natural substrate for polyps of *C. quinquecirrha* (Cargo and Schultz 1966). With nearly 2000 km of riprap, bulkhead, and other shoreline reinforcement structures, and more than 25 000 docks in the tidal waters of the Maryland portion of the bay, the proliferation of hard substrate in Chesapeake Bay and its tributaries has greatly expanded habitat suitable for *C. quinquecirrha* polyps and in some areas may offset the decline in oyster populations.

Artificial structures provide ideal conditions for settlement by jellyfish polyps. Floating docks and crevices

within riprap increase the amount of shaded surfaces of the type that polyps prefer (Pitt 2000; Holst and Jarms 2007). Sea walls and marinas provide shelter in areas that would otherwise be exposed to high wave energy, thereby protecting polyps from being scoured from the surfaces to which they are attached. The rapid colonization and strobilation capacities of polyps (Pitt 2000) enable them to cope with the continuous replacement and maintenance of artificial substrates; at the same time, these disturbances remove the predators and competitors that inhabit similar areas (eg barnacles, sponges, bryozoans, ascidians). Trash materials, which also provide suitable substrates for polyps (eg plastic bags; Tables 1 and 2), collect around artificial structures in harbors (Bulleri and Chapman 2010) and possibly in oceanic areas, as denoted by high densities of suspended plastic materials (Derraik 2002). Ports are often associated with high fishing pressure and turbidity, as well as elevated levels of nutrients, organic matter, and pollutants, thus potentially enhancing polyp food supply and excluding predators and competitors, all of which favors polyp survival and proliferation. Many of these environments have hypoxic bottom waters, to which jellyfish polyps are particularly resistant (Breitburg *et al.* 1997; Purcell *et al.* 2001; Vaquer-Sunyer and Duarte 2008).

Individual polyps multiply asexually through the production of buds and stolons, longitudinal fission, or the formation of podocysts, which are dormant and potentially resistant to stressful conditions such as low food supply and hypoxia (Arai 2009). Juvenile scyphozoan and hydrozoan medusae are produced asexually from the polyps, which can produce as many as 40 ephyrae during each strobilation event (Lucas 2001). Moreover, polyps of many jellyfish species can strobilate repeatedly, are perennial, and can produce new polyps and medusae for years (Arai 1997). Consequently, every new polyp potentially produces hundreds or even thousands of medusae, which then produce thousands or millions of planulae (Boero *et al.* 2008). Medusae are often reported to be abundant in harbors, where artificial substrates abound (Table 1; WebPanel 1; Lotan *et al.* 1994; Purcell 2012); indeed, medusa densities have been shown to decline when artificial substrate is removed (Lo *et al.* 2008). Thus, as asexual production by polyps is believed to be a key driver of medusae outbreaks in coastal areas, artificial structures may be acting as nurseries, facilitating jellyfish blooms in adjacent waters.

The increase in frequency of proliferations of the giant (up to 2 m in diameter) jellyfish *Nemopilema nomurai* in East Asian seas arguably represents the most dramatic case of increased jellyfish blooms; this species has caused substantial losses to regional fisheries and has alarmed the public (Kawahara *et al.* 2006). The habitat for polyps of most problematic jellyfish species, such as *N. nomurai*, is still largely unknown; however, the distribution of these jellyfish includes the coasts of the Korean Peninsula, China, and Japan (Kawahara *et al.* 2006), which is perhaps the region of the world experiencing the fastest growth in aquaculture and shipping activities (Duarte *et al.* 2009)

and their associated infrastructures (Purcell *et al.* 2007; Uye 2008). Moreover, the polyps of some jellyfish can attach to and develop on macroalgae, suggesting that the exponential growth of macroalgal aquaculture in China (Duarte *et al.* 2009) may greatly increase the available natural substrate for polyps. Indeed, the expansion of aquaculture along the coast of China may have provided considerable amounts of new habitat for jellyfish polyps in the East China and South China seas (Dong *et al.* 2010).

The expansion of artificial structures in coastal zones increases the probability of planulae encountering suitable settlement habitats, and may explain why coastal jellyfish blooms appear to be more prevalent now than in the past in some areas (Mills 2001; Purcell *et al.* 2007). This hypothesis applies only to jellyfish species with benthic stages and is not applicable to all bloom-forming jellyfish. Unfortunately, demonstrating a direct relationship between ocean sprawl and jellyfish proliferation is precluded by the impracticality of conducting experiments at the appropriate required spatial and temporal scales. Yet, the potential for artificial substrates to serve as a substrate for polyps conducive to jellyfish blooms must be considered in coastal planning. Increased awareness of the possible link between ocean sprawl and jellyfish proliferation should prompt coastal managers to (1) change the design and surface characteristics of artificial structures deployed in the coastal zone, (2) manage associated environmental conditions to reduce those favoring jellyfish polyps (which include high turbidity, high nutrient and organic loads, and hypoxia, often experienced in harbors and other heavily altered environments), and (3) regulate garbage disposal so as to avoid introduction of substrates, such as plastic materials, that can also support jellyfish polyps.

■ Acknowledgements

This research is a contribution to the Global Expansion of Jellyfish Blooms: Magnitude, Causes and Consequences Working Group, supported by the National Center for Ecological Analysis and Synthesis (NCEAS is supported by the National Science Foundation [grant #DEB-94-21535], the University of California at Santa Barbara, and the State of California) and the Evaluation of Ecosystem Impacts of Global Change in Mediterranean Ecosystems (MEDEICG) project, funded by the Spanish National Plan of I+D (CTM2009-07013). The *C. quinquecirrha* experiments were conducted by DB and JM and supported by National Oceanic and Atmospheric Administration grant #NA09NOS4780214 to DB. We thank K Davies for artistic work.

■ References

- Arai MN. 1997. A functional biology of Scyphozoa. London, UK: Chapman & Hall.
- Arai MN. 2009. The potential importance of podocysts to the formation of scyphozoan blooms: a review. *Hydrobiologia* 616: 241–46.
- Barnes DKA. 2002. Biodiversity: invasions by marine life on plastic debris. *Nature* 416: 808–09.

- Boero F, Bouillon J, Gravili C, *et al.* 2008. Gelatinous plankton: irregularities rule the world (sometimes). *Mar Ecol-Prog Ser* **356**: 299–310.
- Bordehore C, Fuentes VL, Atienza D, *et al.* 2011. Detection of unusual presence of the cubozoan *Carybdea marsupialis* in shallow beaches at the locality of Denia (south-western Mediterranean). *Mar Biodivers Rec* **4**: e69; doi:10.1017/S1755267211000650.
- Breitburg DL, Loher T, Pacey CA, *et al.* 1997. Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. *Ecol Monogr* **67**: 489–507.
- Breitburg DL and Fulford RS. 2006. Oyster-sea nettle interdependence and altered control within the Chesapeake ecosystem. *Estuar Coast* **29**: 776–84.
- Bulleri F and Chapman MG. 2010. The introduction of coastal infrastructure as a driver of change in marine environments. *J Appl Ecol* **47**: 26–35.
- Cargo DG and Schultz LP. 1966. Notes on the biology of the sea nettle, *Chrysaora quinquecirrha*, in Chesapeake Bay. *Chesapeake Science* **7**: 95–100.
- Derraik JGB. 2002. The pollution of the marine environment by plastic debris: a review. *Mar Pollut Bull* **44**: 842–52.
- Di Camillo C, Bettia F, Boa M, *et al.* 2009. Contribution to the understanding of seasonal cycle of *Aurelia aurita* (Cnidaria: Scyphozoa) scyphopolyps in the northern Adriatic Sea. *J Mar Biol Assoc UK* **90**: 1105–10.
- Dong Z, Liu D, and Keesing JK. 2010. Jellyfish blooms in China: dominant species, causes and consequences. *Mar Pollut Bull* **60**: 954–63.
- Duarte CM, Holmer M, Olsen Y, *et al.* 2009. Will the oceans help feed humanity? *BioScience* **59**: 967–76.
- Fuentes V, Straehler-Pohl I, Atienza D, *et al.* 2011. Description of the life cycle of the jellyfish *Rhizostoma pulmo* (Scyphozoa: Rhizostomeae) including information about its distribution, seasonality and inter-annual variability in the Catalan coast and the Mar Menor (Spain, NW Mediterranean). *Mar Biol* **158**: 2247–66.
- Graham WM and Bayha KM. 2007. Biological invasions by marine jellyfish. In: Nentwig N (Ed). *Biological invasions*. Berlin, Germany: Springer-Verlag.
- Guenther J, Misimi E, and Sunde LM. 2010. The development of biofouling, particularly the hydroid *Ectopleura larynx*, on commercial salmon cage nets in Mid-Norway. *Aquaculture* **300**: 120–27.
- Holst S and Jarms G. 2007. Substrate choice and settlement preferences of planula larvae of five Scyphozoa (Cnidaria) from German Bight, North Sea. *Mar Biol* **151**: 863–71.
- Hoover RA and Purcell JE. 2009. Substrate preferences of scyphozoan *Aurelia labiata* polyps among common dock-building materials. *Hydrobiologia* **616**: 259–67.
- Ishii H, Ohba T, and Kobayashi T. 2008. Effects of low dissolved oxygen on planula settlement, polyp growth and asexual reproduction of *Aurelia aurita*. *Plankton Benthos Res* **3**: 107–13.
- Ishii H and Katsukoshi K. 2010. Seasonal and vertical distribution of *Aurelia aurita* polyps on a pylon in the innermost part of Tokyo Bay. *J Oceanogr* **66**: 329–36.
- Johnston EL and Keough MJ. 2000. Field assessment of effects of timing and frequency of copper pulses on settlement of sessile marine invertebrates. *Mar Biol* **137**: 1017–29.
- Kawahara M, Uye S-I, Ohtsu K, and Iizumi H. 2006. Unusual population explosion of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in East Asian waters. *Mar Ecol-Prog Ser* **307**: 161–73.
- Kikinger R. 1992. *Cotylorhiza tuberculata* (Cnidaria: Scyphozoa) – life history of a stationary population. *Mar Ecol* **13**: 333–62.
- Kozloff EN. 1983. *Seashore life of the Northern Pacific Coast*. Seattle, WA: University of Washington Press.
- Lo W, Purcell JE, Hung J, *et al.* 2008. Enhancement of jellyfish (*Aurelia aurita*) populations by extensive aquaculture rafts in a coastal lagoon in Taiwan. *ICES J Mar Sci* **65**: 453–61.
- Lotan A, Fine M, and Ben-Hillel R. 1994. Synchronization of the life cycle and dispersal pattern of the tropical invader scyphomedusan *Rhopilema nomadica* is temperature dependent. *Mar Ecol-Prog Ser* **109**: 59–65.
- Lucas CH. 2001. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia* **451**: 229–46.
- Matsumura K, Kamiya K, Yamashita K, *et al.* 2005. Genetic polymorphism of the adult medusae invading an electric power station and wild polyps of *Aurelia aurita* in Wakasa Bay, Japan. *J Mar Biol Assoc UK* **85**: 563–68.
- Mianzan H. 1989. Scyphomedusae de la Bahía Blanca. *Boletim do Instituto Oceanográfico de Sao Paulo* **37**: 29–32.
- Mills CE. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* **451**: 55–68.
- Miyake H, Terazaki M, and Kakinuma Y. 2002. On the polyps of the common jellyfish *Aurelia aurita* in Kagoshima Bay. *J Oceanogr* **58**: 451–59.
- Pister B. 2009. Urban marine ecology in southern California: the ability of riprap structures to serve as rocky intertidal habitat. *Mar Biol* **156**: 861–73.
- Pitt KA. 2000. Life history and settlement preferences of the edible jellyfish *Catostylus mosaicus* (Scyphozoa: Rhizostomeae). *Mar Biol* **136**: 269–80.
- Purcell JE. 2012. Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Ann Rev Mar Sci* **4**: 209–35.
- Purcell JE, Breitburg DL, Decker MB, *et al.* 2001. Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. In: Rabalais NN and Turner RE (Eds). *Coastal hypoxia: consequences for living resources and ecosystems*. Washington, DC: American Geophysical Union.
- Purcell JE, Hoover RA, and Schwarck NT. 2009. Interannual variation of strobilation by the scyphozoan *Aurelia labiata* in relation to polyp density, temperature, salinity, and light conditions in situ. *Mar Ecol-Prog Ser* **375**: 139–49.
- Purcell JE, Uye S-I, and Lo WT. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Mar Ecol-Prog Ser* **350**: 153–74.
- Schroeder A, Orejas C, and Joschko T. 2006. Benthos in the vicinity of the piles: FINO 1 (North Sea). In: Koller J and Koppel P (Eds). *Offshore wind energy: research on environmental impacts*. Berlin, Germany: Springer-Verlag.
- Uye S-I. 2008. Blooms of the giant jellyfish *Nemopilema nomurai*: a threat to the fisheries sustainability of the East Asian Marginal Seas. *Plankton Benthos Res* **3**: 125–31.
- Vaquer-Sunyer R and Duarte CM. 2008. Thresholds of hypoxia for marine biodiversity. *P Natl Acad Sci USA* **105**: 15452–57.
- Waltham NJ and Connolly RM. 2011. Global extent and distribution of artificial, residential waterways in estuaries. *Estuar Coast Shelf S* **94**: 192–97.
- Willcox S, Moltschanowskyj NA, and Crawford CM. 2008. Population dynamics of natural colonies of *Aurelia* sp scyphistomae in Tasmania, Australia. *Mar Biol* **154**: 661–70.

⁵Shannon Point Marine Center, Western Washington University, Anacortes, WA; ⁶Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Japan; ⁷Dauphin Island Sea Lab, Dauphin Island, AL; ⁸Fisheries Centre, University of British Columbia, Vancouver, British Columbia, Canada; ⁹Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT; ¹⁰California Institute of Technology, Pasadena, CA; ¹¹Marine Biological Station, National Institute of Biology, Piran, Slovenia; ¹²Woods Hole Oceanographic Institution, Woods Hole, MA; ¹³CONICEPT-Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina; ¹⁴Institut de Ciències del Mar, Barcelona, Spain; ¹⁵Smithsonian Environmental Research Center, Edgewater, MD; ¹⁶Department of Marine Science, University of Southern Mississippi, Stennis Space Center, MS; †(deceased)

WebPanel 1. Data on surveys reported in Table 1**Hiroshima Bay, Japan**

- (1) Sampled 2003–present
- (2) Effort: dives per year; two persons \times 5–15 dives \times two tanks (~2 hours) per dive
- (3) Total: 320 person-hours of diving
- (4) Key findings: in 2003 and 2004, we dove mainly along natural rocky and boulder shores and in eelgrass bed areas, in addition to ripraps (hewn stones) and tetrapods (four-legged concrete structures) around the concrete breakwaters. Nevertheless, we could not find any polyps on the exposed substrates. In 2005, we dove both outside (with natural boulders, ripraps, tetrapods) and inside (with ripraps, vertical concrete walls, piles and chains of floating piers, the underside of floating piers, buoys, and old, unused boats) local fishing ports and found many polyps, but only inside the ports, specifically on the underside of floating piers, buoys, and boats. In 2006–2009, we carried out a similar survey and confirmed that no polyps are found on natural exposed substrate, such as rocks and boulders; only a few were found on the vertical concrete walls, while many were located underneath the artificial substrates. We also monitored predators of polyps (total of eight species, including a snail, four nudibranchs, two shrimp, and a crab); predators were encountered on the natural hard substrates, but almost none were found in the port area, and there were none underneath the floating substrates. We also found that newly deployed floating piers sustained many polyps (average during summer: 22 polyps cm^{-2} ; Figure 1c), but old ones with thick accumulations of sessile organisms harbored few polyps, indicating that sessile organisms, such as oysters, mussels, and tunicates, displace the polyps of *Aurelia aurita*, possibly because they can filter planulae from the plankton. From 2010 to the present, we have been monitoring the polyp colonies underneath a floating pier (48 m \times 6 m) that was installed in a fishing port in April 2010. The polyp density on this pier ranges seasonally from 1–5 polyps cm^{-2} (only larger polyps were counted due to photographic limitations); estimated numbers of ephyrae released from this pier are 20 million per year. Net sampling showed that ephyra density inside the port was at least three times higher after installation of the pier than before.

Southampton Water, UK

- (1) Sampled once each month between May 2010 and July 2011
- (2) Effort: two individuals sampling for 30 minutes from a surface pontoon (ie not diver surveys)
- (3) Total: 15 observation hours
- (4) Findings: all polyps were found on shells of living mussels attached to the undersides of floating marina pontoons. Other surfaces (ie nearby stone dock wall or on other epifauna) did not have polyps. Polyp abundance ranged from 0.0002–0.6 polyps cm^{-2} .

Horsea Lake, UK

- (1) Sampled by diver survey between June and September 2001
- (2) Effort: 5 \times 1-hour dives by two divers
- (3) Total: 10 hours of diving

- (4) Key findings: polyps were found on mussels attached to the undersides of artificial structures (radar dome, land rover vehicle, platform, boat, etc) placed in the lake. Polyp abundance ranged from 1–9.5 polyps cm^{-2} in June to 9–20.6 polyps cm^{-2} in September. The remainder of the seabed is a mixture of soft mud–shingle sediment and no polyps were found there.

Gulf of Trieste and the northern Adriatic Sea

- (1) Sampled by divers for >10 years (2000–present) searching natural rocky and boulder shores, seagrass beds, and environments probably unsuitable for polyps, such as muddy sediments
- (2) Effort: annual surveys involving three researchers and several students, allocating >100 person-hours per year
- (3) Total: >1000 hours of surveys
- (4) Key findings: numerous transects along the shore and perpendicular to the coast were completed, but scyphozoan polyps were never found on any natural hard substrate. In 2004–2007, several dives (2–3 per season per year) were made near fish farms, but no polyps were detected. During an ecological survey of the port of Koper in 2009, *Aurelia* spp polyps were found, the majority of which were attached to the undersides of oyster shells growing on dock pillars. In March 2010, we began a monthly monitoring program of the polyp population in five marked areas. An additional survey was conducted to determine whether polyps were living on more pillars than the one monitored regularly. The difficulties of working in the port restricted our survey to one pier (built in 1998 and enlarged in 2004, overall comprising 574 pillars). All pillars examined had polyp populations. Monthly surveys showed that the abundance of polyps varied seasonally, from a minimum of six polyps cm^{-2} in late winter to a maximum of 27 polyps cm^{-2} in summer. Strobilation occurred during November–February; the maximum proportion of strobilating polyps (82%) was in November, and the maximum observed number of ephyra disks per polyp was 18. The potential number of ephyrae released from the polyp population in the port of Koper was estimated to be 5×10^{10} ephyrae in November. Net zooplankton samples have been collected bimonthly since 2004 near our oceanographic buoy (http://buoy.mbss.org/portal/index.php?option=com_content&task=view&id=12&Itemid=26), located about 10 miles from the port. *Aurelia* spp ephyrae were detected very rarely in those samples; high ephyra abundances were detected only in net tows taken within the port area. In earlier zooplankton samples, ephyrae of *Pelagia noctiluca* were found in 1978/79 and 1984/85. Recently, zooplankton was also sampled twice (ends of July and November 2004) at 11 locations along three transects from the eastern to western coast of the “open” northern Adriatic. In November, ephyrae were found at five offshore locations and were fairly abundant at one station (0.4 individuals m^{-3} in vertical tows from near bottom to surface). Past samples taken monthly from similar transects in 1978/79 and January 1980 contained no ephyrae offshore in the northern Adriatic. The only documented natural substrate containing *Aurelia* spp polyps in the Adriatic is

continued

WebPanel 1. – continued

found in a marine lake on the southern Adriatic island of Mljet. In 2011, *Aurelia* spp polyps were detected in two other eastern Adriatic ports (Split and Ploče). Polyps were also identified growing beneath oyster shells from photographs of fouling communities taken during an ecological survey of Croatian offshore gas platforms (summer 2011).

Port of Sant Carles de la Rapita, Catalunya, Spain

- (1) Sampled by snorkeling surveys
- (2) Effort: two individuals snorkeling for 2 hours each
- (3) Key findings: *Obelia dichotoma* polyps (hydroids) were found growing on plastic debris in the harbor. *Phylloporhiza punctata* jellyfish were also observed in the harbor. *Obelia dichotoma* hydroid colonies were found attached to a long plastic cover extending along the full length (about 200 m) of a new dock. No *O dichotoma* polyps were observed on other substrates. Most of

the hydroid colonies had several medusa buds that were nearly ready to release medusae and polyps that had clearly just released medusae. Plankton samples collected in the harbor with a small bongo net of 200- μm mesh size revealed *O dichotoma* medusa density to be 4 individuals m^{-3} .

Mar Menor, Murcia, Spain (*Cotylorhiza tuberculata* polyps)

- (1) Sampled by SCUBA divers
- (2) Effort: details lost with deceased co-author, F Pagés
- (3) Key findings: after an intensive survey of the lagoon, *Cotylorhiza tuberculata* polyps were found on samples of oyster shells and on piers above abandoned oyster cultures. Pagés (2001) reported that one of the causes of the proliferation of *C tuberculata* in the Mar Menor was the abundance of suitable substrate for the polyps provided by the millions of empty oyster shells on the bed of the lagoon.

WebTable 1. Summary of ANOVA testing the substrate preferences of jellyfish planulae

| Effect | DF | F | P |
|--------------------------------|----|-------|----------|
| <i>Cotylorhiza tuberculata</i> | | | |
| Substrate (S) | 3 | 15.56 | < 0.0001 |
| Position (P) | 1 | 10.48 | 0.0026 |
| S \times P | 3 | 3.8 | 0.0205 |
| <i>Chrysaora quinquecirrha</i> | | | |
| Substrate (S) | 15 | 5.28 | < 0.0001 |
| Light (L) | 1 | 1633 | < 0.0001 |
| S \times L | 15 | 104.8 | < 0.0001 |

Notes: the experiment with *Cotylorhiza tuberculata* involved exposed and sheltered locations; the experiment with *Chrysaora quinquecirrha* involved assessments of the effects of light and darkness. DF = degrees of freedom.

WebReferences

Pagés F. 2001. Past and present anthropogenic factors promoting the invasion, colonization and dominance by jellyfish of a Spanish coastal lagoon. In: Briand F (Ed). Gelatinous zooplankton outbreaks: theory and practice. Monaco-Ville, Principality of Monaco: CIESM. Workshop Series 14.