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Review

To Understand Coral Disease, Look at Coral Cells

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Abstract: Diseases threaten corals globally, but 40 years on their causes remain mostly unknown. We hypothesize that inconsistent application of a complete diagnostic approach to coral disease has contributed to this slow progress. We quantified methods used to investigate coral disease in 492 papers published between 1965 and 2013. Field surveys were used in 65% of the papers, followed by biodetection (43%), laboratory trials (20%), microscopic pathology (21%), and field trials (9%). Of the microscopic pathology efforts, 57% involved standard histopathology at the light microscopic level (12% of the total investigations), with the remainder dedicated to electron or fluorescence microscopy. Most (74%) biodetection efforts focused on culture or molecular characterization of bacteria or fungi from corals. Molecular and immunological tools have been used to incriminate infectious agents (mainly bacteria) as the cause of coral diseases without relating the agent to specific changes in cell and tissue pathology. Of 19 papers that declared an infectious agent as a cause of disease in corals, only one (5%) used microscopic pathology, and none fulfilled all of the criteria required to satisfy Koch's postulates as applied to animal diseases currently. Vertebrate diseases of skin and mucosal surfaces present challenges similar to corals when trying to identify a pathogen from a vast array of environmental microbes, and diagnostic approaches regularly used in these cases might provide a model for investigating coral diseases. We hope this review will encourage specialists of disease in domestic animals, wildlife, fish, shellfish, and humans to contribute to the emerging field of coral disease.

Keywords: coral, disease, pathology, diagnostics, epizootiology

Introduction

Corals are colonial animals that belong to the phylum Cnidaria comprising organisms like jellyfish, anemones, and hydra that form polyps with stinging cells. Hard (scleractinian) corals secrete a skeleton of calcium carbonate whereas soft corals (e.g., sea fans), polyps secrete a proteinaceous skeleton (Hyman 1940). Because of their greater abundance and diversity (De'ath and Fabricius 2001), hard corals with their myriad morphologies are the foundation of many coral reefs and are archetypal "ecosystem engineers" (Jones et al. 1994) responsible for building structures ranging from isolated tropical atolls to the Great Barrier Reef (Fig. 1). Tropical coral reefs comprise $<0.2\%$ of the globe's surface area but contain ca. 25% of the earth's biodiversity (Spalding and Grenfell 1997; Pandolfi et al. 2003; Willig et al. 2003). Coral reefs provide food for various fish and invertebrates along with the three-dimensional structure that serves as shelter and habitat for adult and larval fish. Corals also play a

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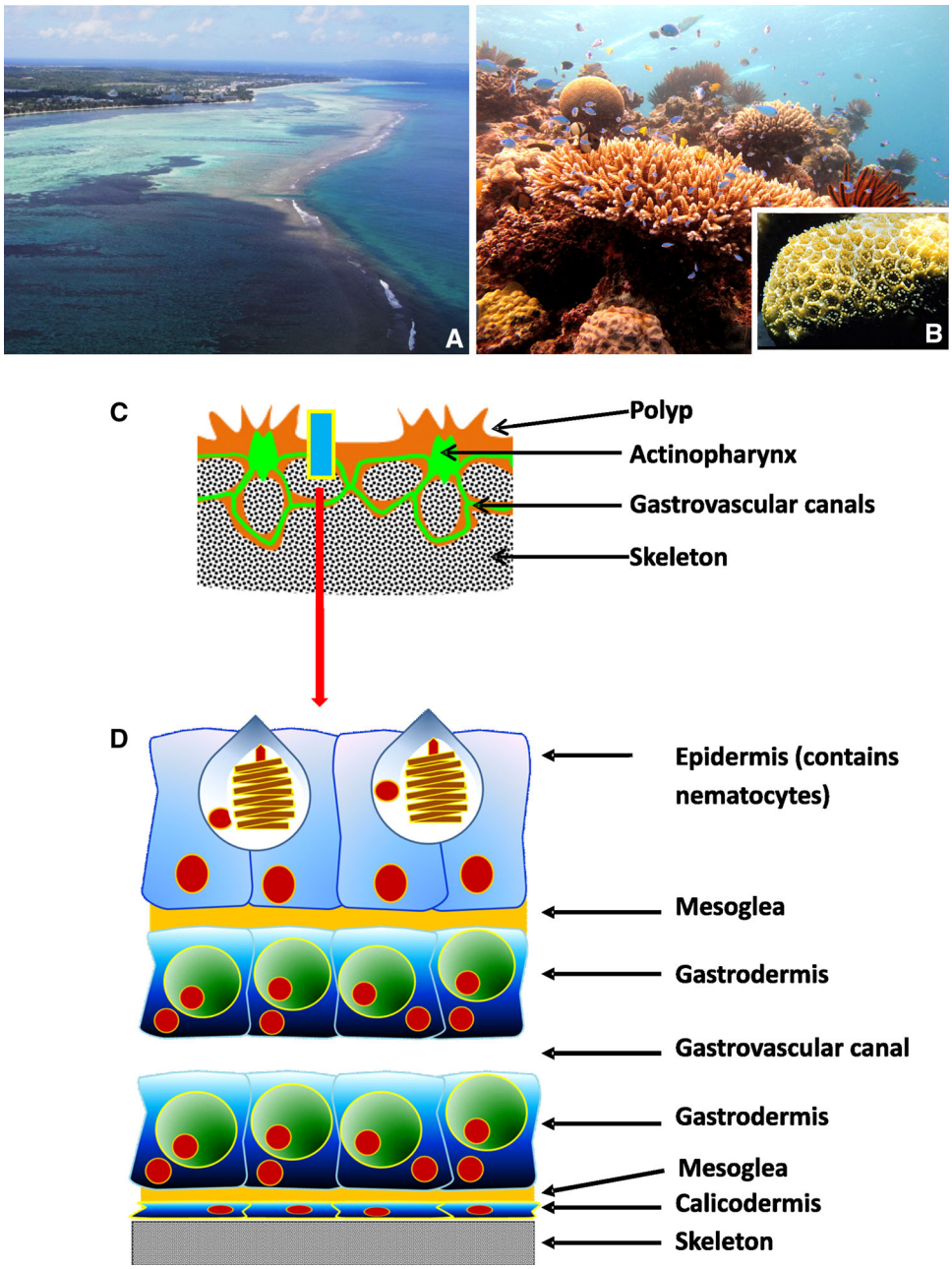

Figure 1. Corals are cnidaria related to jellyfish and anemones that form the foundation of many tropical islands and barrier reefs that can span hundreds of kilometers (**a**). Corals provide the fundamental structure of coral reefs and serve as shelter and food for many marine organisms (**b**). For hard (sleractinian) corals, the animal consists of thousands of interconnected polyps comprising a ca. 0.5- to 1-cm-thick layer of tissue that, sits atop a calcium carbonate skeleton (**b** *inset*). Cutaway diagram of a typical coral (**c**); each polyp has a mouth ringed with tentacles that leads to a pouch called an actinopharynx (primordial stomach), and polyp actinopharyringes are connected to each other by a gastrovascular canal network. Diagram of cell layers (**d**) in small *blue rectangle* outlined in **c**. Epidermis contains stinging cells (nematocysts with coiled barbs characteristic of cnidaria) and other supporting cells. Gastrodermal cells contain intracytoplasmic unicellular symbiotic algae (zooxanthellae), and calicodermis bioconcentrates calcium from seawater to form the skeleton. Mesoglea is a collagenous connective tissue layer separating epidermis from gastrodermis and gastrodermis from calicodermis. Corals have mucus- and for some species, tissue-associated microbiota (Work and Aeby 2014). Further details on microscopic anatomy of corals are available elsewhere (Galloway et al. 2006) (Color figure online).

fundamental geochemical role in tropical oceans by fixing nitrogen and sequestering carbon into their skeletons (Wild et al. 2011). Economically, tropical coral reefs are a source of pharmaceuticals and income from fisheries and tourism, and their massive skeletons also act as protective barriers attenuating wave-induced effects of hurricanes on coastal communities (Moberg and Folke 1999).

Corals are declining globally because of habitat degradation, climate change, overfishing, and disease (Carpenter et al. 2008). Because corals provide the foundation of tropical marine ecosystems (Hughes 1994), their loss leads to extirpation of multiple clades of invertebrates, fish, and top level predators that depend on the coral for sustenance, shelter, foraging, resting, and breeding habitat. For example, in the Caribbean, diseases have led to replacement of two dominant arborescent species of the genus *Acropora* with low encrusting *Agaricia* (Aronson et al. 1998; Aronson and Precht 2001) resulting in loss of three-dimensional structure and marine biodiversity (Graham et al. 2006). In terrestrial ecosystems, the situation is analogous to destroying a tropical forest and replacing it with rangeland. Diseases are also emerging in coral reefs in the Pacific (Willis et al. 2004), where in regions like the Great Barrier Reef, coral cover has declined by 50% over the past 27 years (De'ath et al. 2012). Over time, losses due to disease will likely play a proportionally greater role in degradation of tropical marine habitats, and coral reefs could reach a tipping point (Barnosky et al. 2012) where declines become irreversible (Pandolfi et al. 2005).

Diseases in wildlife can often be traced to a disturbance in balance among agent, host, and environment (Martin et al. 1987). Infectious diseases rarely extirpate populations except in extreme cases such as those affecting rare or endangered animals (De Castro and Bolker 2005). If a species becomes extinct, the environment generally persists. However, tropical corals present a singular case in wildlife disease ecology, because the animal (the coral) is the environment, and the loss of corals has amplifying effects throughout the biological and physical components of the environment (Wild et al. 2011); if you lose corals, you essentially lose the ecosystem. Yet, in spite of increasing research, the causes of most coral diseases are still unknown.

Wildlife Disease Investigation Paradigm

Investigating cause of death in free-ranging wildlife is a deductive process that follows a series of logical steps systematically applied to weigh possible explanations of the mortality. Over the past 70 year, a standardized biomedical approach (Wobeser 2007) to disease investigations involving (1) field investigations, (2) microscopic pathology, (3) laboratory biodetection, and (4) infection trials to fulfill Koch's postulates has successfully been applied to determine cause of wildlife diseases in a variety of organisms and ecosystems.

White-nose syndrome (WNS) in bats in North America provides a recent example. The disease emerged in 2007, and by winter 2008 had killed hundreds of thousands of hibernating bats. In 2007 and early 2008, before a systematic diagnostic approach was adopted, erroneous fungal etiologies were being assigned to WNS because these fungi were easy to culture and identify by standard methods and were common environmental flora. There was also speculation that the fungal growth on the skin of the bats was a secondary invader or postmortem growth and not the primary cause of death. It was only after a systematic approach was applied to this disease that the true cause was identified. This approach included careful histologic description of the unique skin pathology and the anatomy of the fungus causing that pathology in bats with WNS. With that information, the likely cause of WNS was identified by comparing the morphology of conidia and hyphae of the fungi cultured to those of the fungus in the histologic sections of bat skin (Blehert et al. 2009; Meteyer et al. 2009). Indeed, as part of this study, 30 different genera of fungi and 23 different genera of bacteria were isolated from these bats (National Wildlife Health Center unpublished data). This newly identified fungus was named *Geomyces destructans* (Gargas et al. 2009) subsequently reclassified as *Pseudogymnoascus destructans* (Minnis and Lindner 2013). Notably, this fungus was not included in any of the previously proposed causes of WNS, and samples sent for deep sequencing in an effort to identify pathogen genomes did not identify *P. destructans*. Koch's postulates were fulfilled using *P. destructans* to experimentally infect bats and reproduce the disease, with histologic confirmation of the same fungal WNS lesions in both the field and experimentally infected bats and re-isolation of the organism in hibernating bats (Blehert et al. 2009; Lorch et al. 2011).

Current Coral Disease Investigation Paradigm

In contrast, we have known about coral diseases for over 40 years (Sutherland et al. 2003), but we know little about

their causes (Pollock et al. 2011). To assess how diseases in this animal group were being investigated, we searched Google Scholar for terms in the title or text commonly used to refer to various coral diseases (Sutherland et al. 2003): "coral disease," "white syndrome," "white plague," "black band," "yellow blotch," "yellow band," "sea fan aspergillosis," "dark spot," "coral bleaching," "white pox coral," "coral ciliate," "coral fungus," and "coral virus." Publications cited in the reference sections of major reviews on coral diseases were also included (Table S1). To make the search manageable, studies involving bleaching of corals not attributed to infectious agents were excluded as were studies documenting coral mortality subsequent to bleaching. Bleaching in corals is a condition whereby symbiotic algae are expelled leading to loss of color in coral tissues (van Oppen et al. 2009).

For each publication, methods and results were examined for the presence or absence of investigative methods commonly used in animal diseases (field investigation, microscopic pathology, biodetection, experimental infection or observations of disease progression in the laboratory or field, and fulfilling Koch's postulates). *Field investigations* comprised photodocumentation and description of lesions, transects to quantify disease prevalence or progression in the field, or developing models of disease. *Microscopic pathology* included systematic descriptions of lesions at the tissue and cellular level using light or electron microscopy. *Biodetection* included microbial culture, molecular assays, or miscellaneous tests such as zooxanthellae physiology or counts, protein or lipid quantification, measurement of skeletal density or endoliths, or measure of immune mediators. Attempts to infect corals using either cultured microbes or diseased tissues, to transmit disease between lesion and healthy corals by experimental contact, or to monitor progression in diseased corals under various environmental conditions comprised *laboratory trials* if attempts were done in aquaria or *field trials* if attempts were done in the field. *Koch's postulates* included detection of infectious organism associated with cell pathology at the tissue level from field specimens, culture of the organism, experimental infection with replication of lesions at the tissue level similar to those observed in the field, and re-isolation of the organism.

Each publication was evaluated for each of the six categories of diagnostic investigation and assigned a "1" for present or "0" for absent for each category. For example, a paper that had in its methods measurement of coral disease prevalence or progression (field survey), no microscopic pathology, attempts to culture microbes (biodetection), and trials to infect corals in the lab (lab trials) would receive a score of "1" for *Field Investigation*, "0" for *Microscopic Pathology*, "1" for *Biodetection*, "1" for *laboratory trials*, "0" for *field trials*, and "0" for *Koch's postulates*. The total score for each category was divided by the total numbers of papers for all years to arrive at a percentage of diagnostic effort. Data were plotted by year to visualize trends over time for each category of diagnostic effort. Diagnostic categories could not be treated as independent variables and compared because some papers used multiple categories. Accordingly, we focused statistical analyses of temporal trends on microscopic pathology only. To take into account the binary response (presence/absence of diagnostic method), we calculated the percentage of papers that had histopathology done for each year and regressed that percentage versus year using binomial regression (Bolker et al. 2008) with the "glm" function in R (R Development Core Team 2011) weighed by yearly sample size.

Of 492 papers published between 1965 and 2013, field surveys were used in 65% of the papers followed by biodetection (43%), laboratory trials (20%), microscopic pathology (21%), and field trials (9%). Of the microscopic pathology efforts, 57% involved standard histopathology at the light microscopic level (representing 11% of the total diagnostic effort) with the remainder dedicated to electron or fluorescence microscopy. Most (74%) biodetection efforts focused on culture or molecular characterization of bacteria or fungi from corals. Binomial regression of percentage of papers using histopathology over time revealed a significant negative decline (slope = -0.037, $p = 0.0037$) (Fig. 2). No paper fulfilled Koch's postulates, at least as currently practiced in animal medicine. Indeed, of 19 papers where an infectious agent was explicitly declared as cause of disease, only one (5%) made attempts to examine cellular pathology.

We suspect that a primary reason why so little progress has been made in understanding causation of coral disease is that documenting what is happening to sick corals at the cellular level has been overlooked. The literature appears to bear this out in that, compared to field surveys or biodetection, microscopic pathology has consistently taken a minor role, and this tool is being used less frequently over time (Fig. 2). In animal disease investigations, microscopic pathology guides laboratory biodetection using a deductive process whereby the presence (or lack thereof) of organisms associated with cell pathology is confirmed using laboratory

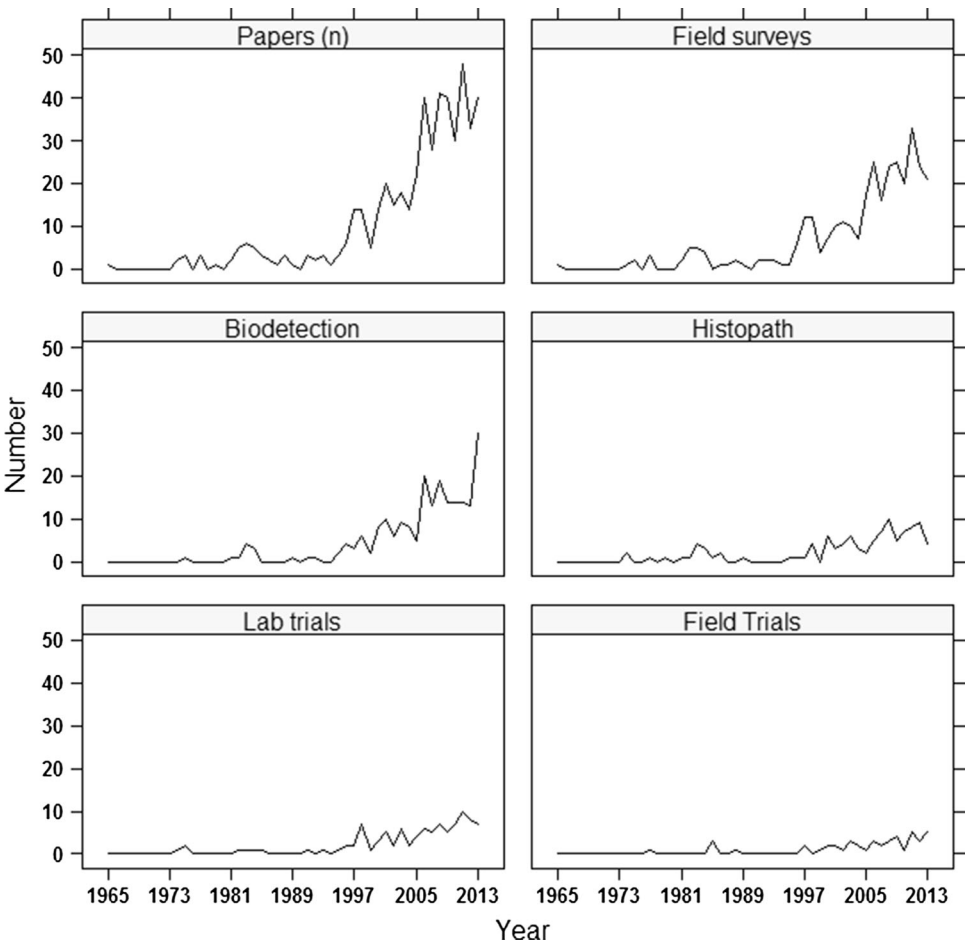

Figure 2. a Total number of papers on coral disease over time and number of papers including particular diagnostic effort on coral disease versus year. Kochs postulates (not graphed) as defined in this paper were not fulfilled in any year. Data are in Table S2.

tests (biodetection). In contrast, coral disease investigations have mostly been inductive, where a microbial etiology is presupposed based on gross observations, and attempts to incriminate said etiology depend mainly on microbial culture and molecular assays with laboratory or field exposure or infection trials to replicate gross lesions. However, in the absence of histopathology to localize pathogen to the characteristic tissue lesion, sampling corals for culture and molecular testing unavoidably samples any micro-organisms in the coral environment along with the coral tissue, all of which could provide misleading results. For example, once a tissue is damaged by any agent (infectious or non-infectious), microbiota will differ between damaged and healthy tissues (Bowler et al. 2001). Although bacteria may be unique to the damaged site, it does not infer that they caused the damage. This, along with the abundant microbes present in the aquatic laboratory or natural marine environment within which the studies are done, can make laboratory replication studies inconsistent and difficult to interpret. Unlike laboratory animals used to study human diseases, corals used for experiments originate from the wild, have an unknown disease history, and are usually not screened for potential pathogens prior to use in experimental infection studies (Work et al. 2011). The lack of standard animal models and standardized growth media also make it challenging to define the cellular pathogenesis of coral disease (Weis et al. 2008). Finally, corals have a host response repertoire limited mainly to growth anomalies, discoloration, or tissue loss (Work and Aeby 2006), and a given gross lesion can have multiple potential etiologic agents that wax and wane over time (Work et al. 2012). Assuming a disease has been experimentally replicated by comparing only grossly visible lesions can be misleading. Attempts to replicate disease in field settings by seeding wild corals with laboratory-raised pathogens or grafting healthy and diseased fragments risks exacerbating disease in wild populations. Finally, such experiments are hard to interpret given the lack of controlled environments and potential confounders.

In summary, without the histology component of the data that provides insight into cell pathology and host response at the microscopic level, documentation of the

relationship between the host, agent, and environment is incomplete. Approaches used in corals contrast with defined experiments in vertebrates that depend heavily on documentation of histopathology and pathogenesis of disease at the tissue and cellular level to fulfill Koch's postulates (Lorch et al. 2011). Ideally, laboratory infection trials would be done on well-defined coral cultures, inoculation of the suspect agent would produce gross and microscopic lesions that match those seen in wild diseased corals, the suspect agent would be directly associated with the tissue damage, and the agent would be re-isolated from diseased tissue.

A Way Forward

Tissue sampling and fixation for histopathology are easy to do in remote situations that lack refrigeration, and archived paraffinized tissue can be used for additional applications such as immunohistochemistry, in situ hybridization, and retrospective studies when new diagnostic techniques become available. Guides for systematically describing gross lesions in corals without inferring causation exist (Work and Aeby 2006; Raymundo et al. 2008). Guides to systematically define coral lesions at the microscopic level are also critical to the characterization of natural or experimentally induced disease (Galloway et al. 2006). Histopathology is currently the only available diagnostic tool that can reveal both the relationship between the potential pathogen and the site of tissue damage along with host response to that pathogen. For instance, histology has been used successfully to identify fungi associated with discoloration in corals (Mydlarz et al. 2008; Work et al. 2008a), and bacteria (Peters et al. 1983) and parasites (Cheng and Wong 1974) associated with disease. Histology is also starting to yield information on coral tumors and how corals repair injuries (Work and Aeby 2010; Palmer et al. 2011). Application of histopathology on a temporal sequential basis is revealing new information about potential causes and pathogenesis of coral diseases defined by tissue loss (Work et al. 2012). Histology is even starting to yield new data on the role of microbial-coral symbioses in ecology and evolution of corals (Work and Aeby 2014). Even absence of detectable lesions at the light microscopic level can be informative, because it suggests that organisms isolated or visible on light microscopy (e.g., metazoa, fungi, protozoa, bacteria) are probably not a cause for the changes seen grossly. For example, histology in combination with fluorescent in situ hybridization was used to refute the hypothesis that bacteria cause tissue loss in the coral *Acropora* affected by "white syndrome" (Ainsworth et al. 2007).

Other approaches such as molecular genomics (Pollock et al. 2011) and immunological (Palmer et al. 2008) tools have been proposed as a way forward to enhance our understanding of coral disease, but these tools cannot be interpreted in the absence of the more complete diagnostic picture, including histopathology. Molecular-based detection methods can detect pathogens and can provide evidence of gene viability, but are generally used to find specific organisms the user previously suspects are present. Culture-based methods provide evidence that viable microorganisms are present but, like molecular methods, fail to connect tissue pathology with the micro-organism and do not define the cellular host response. The presence of viral-like particles in electron microscopy in the absence of supportive evidence of virus-induced pathology at the EM and microscopic level (e.g., vacuolation, inclusions, necrosis, syncytia) can be misleading as it is often difficult to differentiate artifacts from viruses (Crang and Klomparens 1988).

Tools to assess immune response in corals show great promise to complement histopathology and enhance our understanding of disease pathogenesis by illustrating how the coral host responds to various insults (Palmer and Traylor-Knowles 2012). However, immune assays without histopathology are unlikely, in the near future, to shed light on actual cause of disease unless the disease is a primary immune dysfunction. The immune response is highly variable even in well-characterized animals such as laboratory mice (Keil et al. 2001), and attempts to assess immune function in wildlife have met with mixed results because of both the lack of available immune assays and the host responses varies with the pathogen, dose, reproductive cycle of host, and other factors. Our knowledge of cnidarian immune response systems and physiology is limited (Mydlarz et al. 2006), and there is no widely accepted animal model for coral disease (Weis et al. 2008).

There is a disconnect between the training received by researchers that specialize in infectious disease (typically vertebrate diseases) and the training received by researchers that specialize in the biology and ecology of corals. For animal diagnosticians, corals are not conventional animals. Corals live in an environment that makes it difficult to investigate or even detect disease, and they do not have complex internal organs such as liver and kidneys. However, the approach to coral disease pathology and pathogenesis, could be modeled on structures more familiar to animal disease diagnosticians such as mucous membranes, the gut, or skin (Fig. 3). Just as diseases of the epidermis

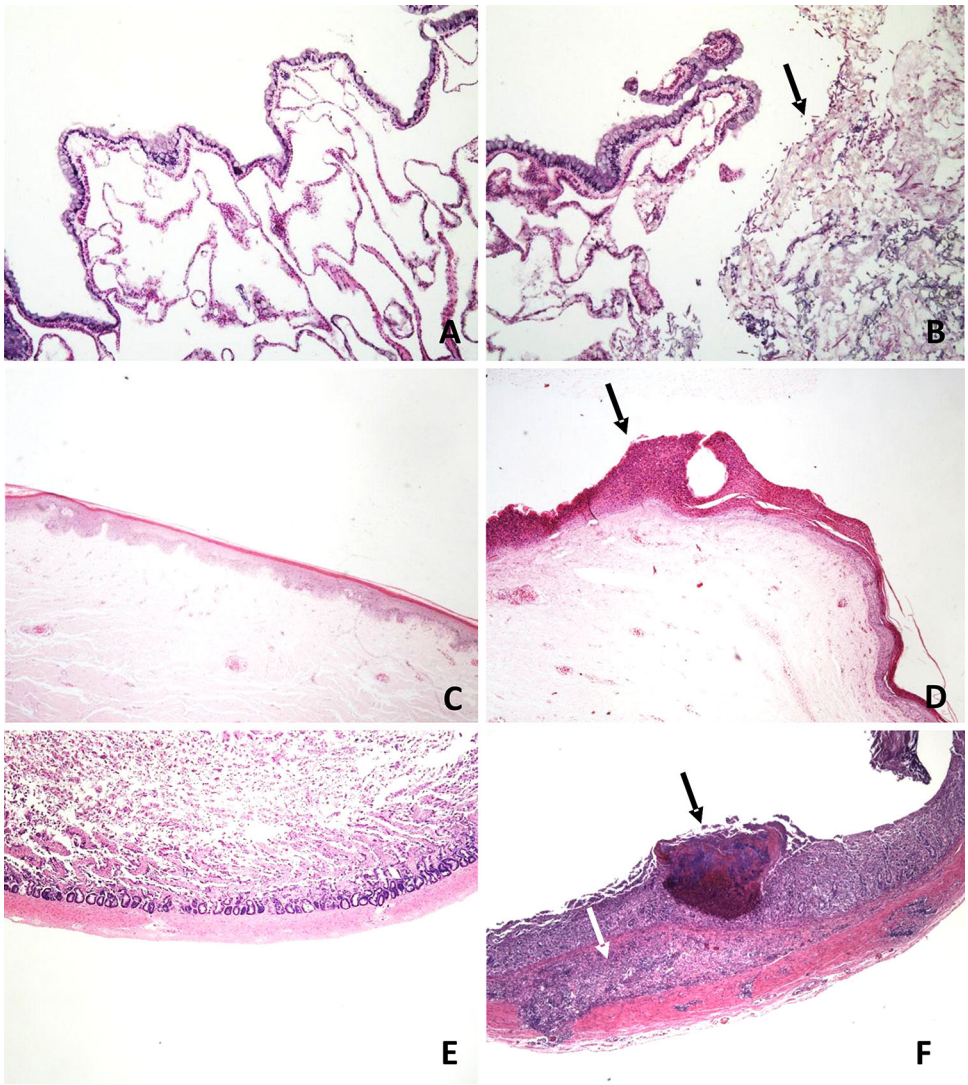

Figure 3. Like the gut or the skin (Guarner and Malagelada 2003), coral mucus has its own associated microbiota that changes with disease (Wilson et al. 2012) and can be closely tied to the symbiotic algae (Littman et al. 2010). Because corals resemble epithelial surfaces, gross, and microscopic pathology in these animals can be approached similarly to that of the skin or gut. **a** Normal cellular morphology of the coral *Montipora capitata* and **b** necrosis (*arrow*) associated with invasion of mixed fungi and cyanobacteria; **c** normal skin from an olive ridley turtle (*Lepidochelys olivacea*) and **d** Erosion and necrosis of epidermal surface (*arrow*); **e** normal gut mucosa from a Hawaiian goose (*Nesochen hawaiiensis*); and **f** focal mucosal necrosis associated with microcolonies of bacteria (*black arrow*) and marked inflammation of mucosa and smooth muscle (*white arrow*). Note that all three animals manifest a similar basic host response (necrosis) associated with cyanobacteria in the case of the coral (**b**) or bacteria in case of the goose (**f**). Unlike reptiles or birds, however, many corals have a limited inflammatory response, and that can make interpretation of histopathology challenging (Color figure online).

and mucosal surfaces often have similar gross lesions with different causes, so do corals. Similarly, both have consortia of normal microbiota.

These are good arguments for building teams of researchers with multiple expertise that can maximize the opportunities for coral disease investigations. Researchers that specialize in the infectious diseases of humans, domestic animals, wildlife, fish, and invertebrates have a lot to offer to the coral disease community. With the proper partnerships, there is the potential for major breakthroughs in our understanding of how disease operates in corals at the cellular and tissue level that would further strengthen the links between pathogen, host disease, and environmental influence. If we can determine what kills corals and how to mitigate those causes of mortality, we not only save an animal but potentially an entire ecosystem. There are

currently no other situations where systematic application of a standard diagnostic approach could have such a profound impact on wildlife conservation (Work et al. 2008b). Because of the nascent nature of this discipline and the novel situations posed by corals, many challenging and exciting discoveries await those willing to take the plunge.

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Table S1. List of review/synthesis papers used for literature analysis[1-38].

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Table S2. List of publications, year of publication, whether or not a categorical declaration of causation was made (Cause), and six categories of effort (Bold type) including field surveys (photos, transects, modeling), pathology, biodetection (culture, molecular, miscellaneous), lab and field trials (experimental infection and gross observation), and Koch's postulates.

Reference	YEAR	CAUSE	**SURVEY**	**HISTOPATH**	Histopathology	Other	**BIOEDECTION**	Culture	Molecular	Miscellaneous	**LAB TRIAL**	**FIELD TRIAL**	**KOCHS**
1	2002		0	0		1	0				1	0	0
2	2003		1	0		1	0				0	0	0
3	2008		1	1	x	1	0				0	0	0
4	1991		0	0		1	0				1	0	0
5	1998		1	0		1	0				1	0	0
6	2005		1	0		1	0				0	0	0
7	2007		1	0		1	0				0	0	0
8	2011		1	0		1	0				0	0	0
9	2010		1	0		1	0				1	0	0
10	2006		0	0		1	0				1	0	0
11	2011		1	0		1	0				0	0	0
12	2011		1	0		1	0				0	0	0
13	2006		0	1		1	0				0	0	0
14	2008		1	1	x	x	1		x		0	0	0
15	2007		0	1	x	x	0				0	0	0
16	2006		1	1	x	x	0				0	0	0
17	2011		0	0		1	1	x	x		1	0	0
18	2001		0	0		1	1	x	x		0	0	0
19	2004		0	0		1	1			x	0	1	0
20	2001		1	0		1	0				0	0	0
21	2010		0	0		1	1	x	x		1	0	0
22	2013		1	0		1	0				0	0	0
23	2010		0	1	x	1	0				1	1	0
24	2008		0	0		1	1		x		0	0	0
25	2013		0	0		1	1			x	1	0	0
26	2008		1	0		1	0				0	0	0
27	1977		1	0		1	0				0	0	0
28	1982		1	0		1	0				1	0	0
29	1985		0	0		1	0				1	1	0
30	1985		0	0		1	0				0	1	0
31	1988		0	0		1	0				0	1	0
32	1988		1	0		1	0				0	0	0
33	1999		1	0		1	0				0	0	0
34	2001		1	0		1	0				0	0	0

35	2001		1	0		1	0				0	0	0
36	1998		1	0		1	0				0	0	0
37	2000		1	0		1	0				0	0	0
38	1997		1	0		1	0				0	0	0
39	1998		1	0		1	0				0	0	0
40	1982		1	0		1	0				0	0	0
41	2013		0	0		1	1		x		0	0	0
42	2009		0	1		x	0				0	0	0
43	2010	x	1	0		1	1	x	x		1	0	0
44	2002		1	0		1	0				0	0	0
45	1997		1	0		1	0				0	0	0
46	1998		1	0		1	0				0	0	0
47	2009		0	0		1	1	x	x		0	0	0
48	1983		1	0		1	1			x	0	0	0
49	1982		1	0		1	0				0	0	0
50	2007		1	0		1	0				0	0	0
51	2013		1	0		1	0				0	0	0
52	2000		0	1	x	x	1	x		x	1	0	0
53	2001		0	0		1	1	x			1	0	0
54	2000		0	1	x	x	1	x			1	0	0
55	2001		0	0		1	1	x		x	1	0	0
56	2003		0	0		1	1	x		x	1	0	0
57	2000		0	1	x	x	1	x		x	1	0	0
58	2005	x	0	0		1	1	x	x		1	0	0
59	2007		1	1	x	1	1	x	x		0	0	0
60	2013		1	0		1	1	x	x		0	0	0
61	1999		0	0		1	1	x		x	1	0	0
62	2002	x	0	1		x	1	x	x		1	0	0
63	2003	x	0	0		1	1	x	x		0	0	0
64	2003	x	0	1		x	1	x	x	x	1	0	0
65	2009		1	0		1	0				0	0	0
66	2005		1	1	x	1	1			x	1	0	0
67	2003		1	0		1	0				0	0	0
68	2005		1	0		1	0				0	0	0
69	2005		1	0		1	0				0	0	0
70	2010		0	1	x	1	0				0	0	0
71	2005		1	0		1	0				0	0	0
72	2005		0	0		1	1	x	x		0	0	0
73	2008		1	0		1	1		x	x	0	0	0
74	2013		0	0		1	1	x	x		0	0	0
75	2007		1	0		1	0				1	1	0
76	2009		1	0		1	0				0	0	0
77	2009		1	0		1	0				0	0	0
78	2007		1	0		1	0				0	0	0
79	2012		1	0		1	0				0	0	0
80	2013		1	0		1	0				0	1	0

81	2006		0	0		1	1	x			0	0	0
82	2008		0	0		1	1	x	x		1	0	0
83	1997		1	0		1	0				0	0	0
84	1997		1	0		1	0				0	0	0
85	2000		1	1	x	1	0				0	1	0
86	2006		1	0		1	0				0	0	0
87	2006		1	0		1	0				0	0	0
88	1997		1	0		1	0				0	0	0
89	2009		1	0		1	0				0	0	0
90	2007		1	0		1	0				0	0	0
91	2011		1	0		1	0				0	0	0
92	2003		1	0		1	0				1	1	0
93	2007		1	0		1	0				0	0	0
94	2012		1	1	x	1	1	x	x		1	0	0
95	2013		0	0		1	1		x		0	0	0
96	2004		1	0		1	0				0	0	0
97	2013		0	0		1	1		x	x	0	1	0
98	2011		1	0		1	0				0	0	0
99	2011		1	1	x	1	0				0	0	0
100	1993		1	0		1	0				0	0	0
101	2002		0	1	x	x	0				0	0	0
102	1993		1	0		1	0				0	0	0
103	2008		1	0		1	0				0	0	0
104	2011		0	0		1	1	x	x		0	0	0
105	1995		0	0		1	0				1	0	0
106	2011		1	0		1	0				0	0	0
107	2012		0	0		1	1	x	x		1	0	0
108	2004		0	0		1	1		x		0	0	0
109	2005		1	0		1	0				0	0	0
110	2000		1	1		x	1	x			0	0	0
111	1997		1	0		1	0				0	0	0
112	2001		1	0		1	1			x	0	0	0
113	2012		0	0		1	1	x	x	x	0	0	0
114	2004		0	1	x	x	1	x		x	0	0	0
115	2004		0	0		1	1	x		x	1	0	0
116	2008	x	0	0		1	1	x		x	1	0	0
117	2012		0	1	x	x	0				1	0	0
118	1975		1	0		1	0				0	0	0
119	1974		0	1	x	1	0				0	0	0
120	2012		1	0		1	1	x	x		0	0	0
121	2011		1	0		1	0				0	0	0
122	2013		0	0		1	1	x		x	1	0	0
123	2009		1	0		1	0				1	0	0
124	1994		1	0		1	0				0	0	0
125	1998		1	1	x	1	1			x	0	0	0
126	2013		0	1	x	1	1	x	x		0	0	0

127	2002		0	0		1	1		x		0	0	0
128	2009		0	0		1	1		Zoox		0	0	0
129	2013		1	0		1	1			x	0	0	0
130	2013		0	0		1	1		x		0	0	0
131	2006		1	0		1	1			x	0	0	0
132	2003		1	0		1	0				0	0	0
133	2003		1	0		1	0				0	0	0
134	2009		1	0		1	0				0	0	0
135	2005		1	0		1	0				0	0	0
136	2006		1	0		1	1			x	0	0	0
137	2008		0	0		1	1		x		0	0	0
138	2006		0	0		1	1			x	1	0	0
139	2010		0	0		1	0				1	0	0
140	2006		1	0		1	0				0	0	0
141	2008		1	1		x	0				1	0	0
142	2010		0	0		1	1		x		0	0	0
143	2011		0	0		1	1	x	x	x	0	0	0
144	2003	x	0	1		x	1	x	x		0	0	0
145	2000		1	0		1	0				0	0	0
146	2006		1	1	x	1	1			x	0	0	0
147	2008		1	0		1	0				0	0	0
148	2002		1	0		1	1			x	1	0	0
149	1979		0	1		x	0				0	0	0
150	1977		1	0		1	0				0	1	0
151	1987		1	0		1	0				0	0	0
152	1991		1	0		1	0				0	0	0
153	2009		0	0		1	1	x			1	0	0
154	2007		0	0		1	1	x	Phage		1	0	0
155	2007		1	1	x	1	0				0	0	0
156	1988		1	0		1	0				0	0	0
157	2006		0	0		1	1			x	0	0	0
158	2009		1	0		1	0				0	0	0
159	2005		1	0		1	0				0	0	0
160	2012		1	0		1	0				0	1	0
161	2010		1	0		1	0				0	0	0
162	2008		1	0		1	0				0	0	0
163	2004		0	0		1	1		x		0	0	0
164	2003		0	0		1	1		x		0	0	0
165	2004		0	0		1	1		x		0	0	0
166	2002		1	1		x	1		x		0	0	0
167	2011		0	0		1	1	x			0	0	0
168	2009		0	0		1	1	x		x	0	0	0
169	2003		1	0		1	0				0	0	0
170	2013		0	0		1	1		x		0	0	0
171	2013		0	0		1	1	x			0	0	0
172	1975		1	0		1	0				1	0	0

173	2001		1	0		1	0				0	0	0
174	1992		1	0		1	0				0	0	0
175	2005		1	0		1	0				0	0	0
176	2003		1	1	x	x	1			x	0	1	0
177	1998	x	0	0		1	1		x		1	0	0
178	2012		1	0		1	0				1	1	0
179	2006	x	0	0		1	1	x			0	1	0
180	2007		0	0		1	1	x			0	0	0
181	2001		1	0		1	0				0	0	0
182	2006		0	0		1	1	x			0	0	0
183	1982		1	0		1	0				0	0	0
184	2012		0	0		1	0				1	0	0
185	1984		1	0		1	0				0	0	0
186	1984		0	0		1	1			x	1	0	0
187	1985		0	1	x	x	0				0	1	0
188	1989		1	1	x	1	1			x	0	0	0
189	2008		0	0		1	1			x	0	0	0
190	2006		1	0		1	0				0	0	0
191	2012		1	0		1	1	x	x		0	0	0
192	1982		1	1	x	1	1	x			0	0	0
193	1984		1	1	x	1	1	x			0	0	0
194	1998		1	0		1	0				0	0	0
195	1997		1	0		1	0				0	1	0
196	1996		1	0		1	1			x	0	0	0
197	2011		1	0		1	0				0	0	0
198	2010		1	0		1	0				0	0	0
199	2013		1	0		1	0				0	0	0
200	2007		1	0		1	0				0	0	0
201	2011		1	0		1	0				0	0	0
202	2009		1	0		1	0				0	0	0
203	2008		1	0		1	0				0	0	0
204	2001		1	0		1	0				0	1	0
205	2008		1	0		1	0				0	0	0
206	2010		1	0		1	0				0	0	0
207	2013		0	0		1	1	x			1	0	0
208	2010		1	0		1	0				0	0	0
209	2000		1	0		1	0				0	0	0
210	2012		1	1	x	1	1			x	0	1	0
211	2001		0	1		x	1	x			1	0	0
212	2012		1	0		1	0				0	0	0
213	1974		1	1		1	0				1	0	0
214	2002		1	0		1	0				0	0	0
215	2012		1	0		1	0				0	0	0
216	2004		1	1		x	0				0	0	0
217	2005		1	0		1	0				0	0	0
218	2011		1	0		1	0				0	1	0

219	2007		1	0		1	0				1	0	0
220	2011		1	0		1	0				0	0	0
221	2006		1	0		1	0				0	0	0
222	2005		1	0		1	0				0	0	0
223	2011		1	0		1	0				0	0	0
224	2013		0	0		1	1		x		0	0	0
225	2006		1	0		1	0				0	0	0
226	2004		1	0		1	0				0	0	0
227	2000		0	0		1	1			x	0	0	0
228	2000		0	0		1	1			x	0	0	0
229	2010		1	0		1	1		x		0	0	0
230	2005		0	0		1	1		zoox		1	0	0
231	2011		1	0		1	1		x		0	0	0
232	2006		0	0		1	1	x			1	0	0
233	2011	x	0	0		1	1	x			0	1	0
234	1981		1	0		1	0				0	0	0
235	2000		0	0		1	1	x			0	0	0
236	2002		0	0		1	1			x	0	0	0
237	1998		1	0		1	0				0	0	0
238	2013		1	1	x	x	0				0	0	0
239	2012		0	0		1	1	x			0	0	0
240	2011		1	0		1	0				1	0	0
241	2005		0	0		1	0				1	0	0
242	2001	x	0	1		x	1	x	x		0	0	0
243	1996	x	1	1		x	1	x			1	0	0
244	1998		1	1	x	1	1	x			1	0	0
245	1997	x	1	1	x	x	1	x			1	0	0
246	1996		1	0		1	0				0	0	0
247	2002		1	0		1	0				0	0	0
248	1997		0	0		1	0				0	1	0
249	2010		0	0		1	1		x		0	0	0
250	1995		0	1		x	1			x	0	0	0
251	2011		1	0		1	0				0	0	0
252	2013		0	0		1	1		x		0	0	0
253	2011		1	0		1	0				0	0	0
254	1996		1	0		1	0				0	0	0
255	2011		0	0		1	1			x	1	0	0
256	1984		1	1	x	1	1			x	0	0	0
257	2007		0	1		x	1	x			0	0	0
258	2010	x	1	1		x	1	x			0	0	0
259	2008		1	0		1	0				0	0	0
260	2010		1	0		1	1	x			0	0	0
261	2011		1	0		1	0				0	0	0
262	2006		1	0		1	0				0	0	0
263	2004		1	1	x	x	0				0	0	0
264	2009		1	1		x	0				0	0	0

265	1997		1	0		1	0				0	0	0
266	2009		0	0		1	1	x	x		1	0	0
267	2011		0	1		x	0				1	0	0
268	2012		0	1		x	0				0	0	0
269	2012		0	0		1	1			x	1	0	0
270	2008		1	0		1	0				0	0	0
271	2003		1	0		1	1	x			0	0	0
272	2006		1	0		1	0				0	0	0
273	2002		1	0		1	0				0	0	0
274	2007		1	0		1	0				0	0	0
275	2013		1	0		1	1	x	x		1	0	0
276	1975		0	0		1	1	x			1	0	0
277	2012		1	0		1	0				0	0	0
278	2012		1	0		1	0				0	0	0
279	2013		1	0		1	0				0	0	0
280	2013		1	0		1	1	x	x		0	0	0
281	1981		1	1	x	1	1			x	0	0	0
282	1977		1	1	x	1	0				0	0	0
283	2006		1	0		1	1			x	0	0	0
284	2009		0	0		1	0				0	1	0
285	2011		1	0		1	0				0	1	0
286	2009		1	0		1	1			x	0	0	0
287	2007		0	1	x	1	1	x		x	1	0	0
288	2008		0	1	x	1	1	x		x	1	0	0
289	2009		0	0		1	1	x			0	0	0
290	2007		0	0		1	1	x	x		0	0	0
291	2009		1	0		1	0				0	0	0
292	1997		1	0		1	0				0	0	0
293	1997		1	0		1	0				0	0	0
294	2010		1	0		1	0				0	0	0
295	2013		0	0		1	0				1	0	0
296	2002		1	0		1	0				0	0	0
297	2007		1	0		1	0				0	0	0
298	2009		1	0		1	0				0	1	0
299	2006		1	0		1	0				0	0	0
300	2004		1	0		1	1	x			0	1	0
301	2011		1	0		1	0				0	0	0
302	2006		1	0		1	0				0	0	0
303	2009		1	0		1	0				0	0	0
304	2010		1	0		1	0				0	0	0
305	2008		1	0		1	0				1	1	0
306	2010		0	1	x	1	1			x	0	0	0
307	2011		0	0		1	1			x	0	0	0
308	2010		1	0		1	0				0	0	0
309	2011		0	0		1	1			x	0	0	0
310	2008		0	1	x	1	1			x	0	0	0

311	2009		1	1	x	1	1			x	0	0	0
312	2011		0	1	x	1	0				0	0	0
313	2006		1	0		1	1		x		0	0	0
314	2003		1	0		1	1		x		0	0	0
315	2013		1	1		x	1		x		0	0	0
316	2008		0	1	x	x	0				0	0	0
317	2002	x	1	1		x	1	x	x		0	1	0
318	1984		1	1	x	1	0				0	0	0
319	1986		1	1	x	1	0				0	0	0
320	1983		1	1	x	1	0				0	0	0
321	2003		0	1	x	1	0				0	0	0
322	2006		1	0		1	1	x			0	0	0
323	2007		1	0		1	1	x			0	0	0
324	2013		0	0		1	0				1	0	0
325	2010		0	0		1	1		x		0	0	0
326	2008		0	0		1	1	x	x		0	0	0
327	2001		1	0		1	0				0	0	0
328	2011		1	0		1	0				0	0	0
329	1991		1	0		1	1	x		x	0	0	0
330	1983		1	1	x	1	0				0	0	0
331	2009		0	1		x	1	x	x		0	0	0
332	2002		1	0		1	0				0	0	0
333	2006		0	1	x	1	0				0	0	0
334	2006		1	1	x	x	1			x	1	0	0
335	2001		0	1	x	x	1	x		x	0	0	0
336	2009		1	0		1	0				0	0	0
337	2003		1	1	x	1	0				1	1	0
338	2005		1	0		1	0				0	0	0
339	2013		1	0		1	1			x	0	0	0
340	2006		0	0		1	1	x			0	0	0
341	2008		0	1	x	x	0				0	0	0
342	1992		1	0		1	1			x	0	0	0
343	2003		0	0		1	1	x			0	0	0
344	2001		0	0		1	0				1	0	0
345	1996		1	0		1	1	x			0	0	0
346	1997		1	0		1	1			x	0	0	0
347	1993		0	0		1	0				1	0	0
348	1998		1	1		x	1	x			1	0	0
349	1998	x	0	1		x	1	x			1	0	0
350	1997		0	0		1	1	x			1	0	0
351	2009		0	0		1	1			x	1	0	0
352	2005		0	1		x	1	x	x		0	0	0
353	2007		0	0		1	1	x	x	x	0	0	0
354	2005		1	0		1	0				0	0	0
355	2002		1	0		1	0				0	0	0
356	1995		1	0		1	1	x			0	0	0

357	1998		1	0		1	0				0	0	0
358	2013		0	0		1	1	x	x		0	0	0
359	2008		1	0		1	0				0	0	0
360	2009		0	0		1	0				1	1	0
361	2001		1	0		1	0				0	0	0
362	2006		1	0		1	1			x	0	1	0
363	2011		1	0		1	0				1	1	0
364	2008		0	1		x	1			x	0	0	0
365	2008		1	0		1	1			x	0	0	0
366	2006		1	0		1	0				0	0	0
367	2009		1	0		1	0				0	0	0
368	2005		1	0		1	0				0	0	0
369	1983		0	1		x	1			x	0	0	0
370	1983		1	1		x	1			x	1	0	0
371	2008		0	0		1	1	x			0	0	0
372	2008		0	0		1	1	x	x		0	0	0
373	2008		0	0		1	1		x		0	0	0
374	2010		1	0		1	0				0	0	0
375	2008		1	0		1	0				0	0	0
376	2001		1	0		1	0				0	0	0
377	1999		1	0		1	0				0	0	0
378	2005		1	0		1	0				0	0	0
379	2009		1	0		1	0				0	0	0
380	2011		0	0		1	0				1	0	0
381	2010		1	1	x	1	1		x		0	0	0
382	2011		1	0		1	0				0	0	0
383	2008		0	0		1	1		x		0	0	0
384	2009		0	0		1	1		x		0	0	0
385	2006		0	0		1	1		x		0	0	0
386	2006		1	0		1	0				0	0	0
387	2012		1	0		1	0				0	0	0
388	2013		1	0		1	1	x	x		0	0	0
389	2012		1	0		1	1			x	0	0	0
390	2012		1	0		1	1			x	0	0	0
391	2008		1	0		1	0				0	0	0
392	1999		1	0		1	1	x		x	0	1	0
393	2013		1	1	x	1	0				0	0	0
394	2008		1	0		1	0				0	1	0
395	1998		1	0		1	1		x		1	0	0
396	1996		1	0		1	1	x	x		1	0	0
397	2013		1	0		x	1	x			0	1	0
398	2006		0	0		1	0				1	0	0
399	2010		1	0		1	0				0	0	0
400	2008		1	0		1	0				0	0	0
401	2013		1	0		x	1		x		0	0	0
402	2009		1	0		1	0				0	0	0

403	2012		1	0		1	0				0	0	0
404	2013		0	0		1	1		x		0	0	0
405	1965		1	0		1	0				0	0	0
406	2011		0	0		1	1	x		x	0	0	0
407	2011		1	0		1	0				1	1	0
408	2012		1	1	x	1	0				0	0	0
409	2012		1	1	x	1	0				0	0	0
410	2011		1	0		1	0				0	0	0
411	2009		0	0		1	1		x		0	0	0
412	2006		0	0		1	1	x	x	x	0	0	0
413	2003		1	1		x	0				1	0	0
414	2009		0	0		1	1	x			0	0	0
415	2008	x	1	0		1	1	x	x		1	0	0
416	2010		0	0		1	1	x	x		0	0	0
417	2011	x	1	0		1	1	x	x		1	0	0
418	2013		1	0		1	1		x		0	0	0
419	2012		1	0		1	1		x		0	0	0
420	2013		1	0		x	1	x	x		0	0	0
421	2013		0	0		1	1		x		0	0	0
422	2013		1	0		1	1				0	0	0
423	1983		1	0		1	1	x			0	0	0
424	2013		1	0		1	0				0	0	0
425	2011		1	0		1	0				0	0	0
426	2001		0	0		1	1	x	x		0	0	0
427	2006		0	0		1	1	x	x		0	0	0
428	2007		0	0		1	1	x	x		0	0	0
429	2008		0	0		1	1	x	x		0	0	0
430	2013		1	0		1	1	x			0	1	0
431	2007		1	0		1	0				0	0	0
432	2009		1	0		1	0				0	0	0
433	2001		0	0		1	1		zoox		1	1	0
434	1998		1	0		1	0				1	0	0
435	2007		0	1		1	1			x	0	0	0
436	1986		0	1	x	1	0				0	0	0
437	2012		0	0		1	1	x	x		1	0	0
438	2009		1	0		1	0				0	0	0
439	2007		0	1	x	1	0				0	0	0
440	2008		1	0		1	0				0	0	0
441	2010		1	0		1	1	x	x		1	0	0
442	2011		0	1	x	x	1	x	x	x	1	0	0
443	2011		0	1		x	1	x	x		1	0	0
444	2006		0	0		1	1	x	x		0	0	0
445	2000		0	0		1	0				0	1	0
446	2010		0	0		1	1	x	x		0	0	0
447	2008		1	0		1	0				0	1	0
448	2007		0	0		1	1	x	x		0	1	0

449	2006		1	0		1	0				0	0	0
450	2006		1	0		1	1	x	x		1	1	0
451	2009		0	0		1	0				0	1	0
452	2004		1	0		1	0				0	0	0
453	2007		1	0		1	0				0	0	0
454	2007		0	0		1	1			x	1	0	0
455	2006		1	0		1	0				0	0	0
456	2011		1	0		1	0				0	0	0
457	2009		1	0		1	0				0	0	0
458	2009		1	0		1	0				0	0	0
459	2009		1	1	x	1	0				0	0	0
460	2012		1	0		1	0				0	0	0
461	2008		0	0		1	1	x	x		1	0	0
462	2000		1	0		1	0				0	0	0
463	2004		0	0		1	1	x	x		1	0	0
464	2005		1	0		1	0				0	1	0
465	2012		1	0		1	0				0	0	0
466	1999		1	0		1	0				0	0	0
467	2010		1	0		1	0				0	0	0
468	2011		1	0		1	0				0	0	0
469	2011		1	1	x	1	0				0	0	0
470	2010		1	1	x	1	0				0	0	0
471	2012		0	0		1	1	x	x		0	0	0
472	2004		1	0		1	0				0	0	0
473	2006		1	0		1	0				0	0	0
474	2010		1	1	x	1	0				1	0	0
475	2011		1	1	x	1	0				0	0	0
476	2008		1	1	x	1	0				0	0	0
477	2008		1	1	x	1	0				0	0	0
478	2011		0	1	x	x	1		x	x	0	0	0
479	2005		1	0		1	0				0	0	0
480	2012		1	1	x	1	0				0	0	0
481	2011		1	0		1	0				0	0	0
482	2009		1	0		1	1			x	0	0	0
483	2001		0	0		1	1			x	0	0	0
484	2000		1	1	x	1	1			x	0	0	0
485	2007		1	0		1	1	x			0	0	0
486	2012		1	1	x	x	0				0	0	0
487	2012		1	1	x	x	0				1	0	0
488	2011		1	0		1	0				0	0	0
489	2013	x	0	0		1	1	x	x		1	1	0
490	2012		1	0		1	0				0	0	0
491	2010		1	0		1	1	x	x		0	0	0
492	2009		1	0		1	0				0	0	0

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