Pauly, D. V. Christensen, S. Guénette T.J. Pitcher, U.R. Sumaila, C.J. Walters, R. Watson and D. Zeller. 2002. Toward sustainability in world fisheries. *Nature* 418: 689-695.

## insight review articles

# Towards sustainability in world fisheries

Daniel Pauly, Villy Christensen, Sylvie Guénette, Tony J. Pitcher, U. Rashid Sumaila, Carl J. Walters, R. Watson & Dirk Zeller

Fisheries Centre, University of British Columbia, 2204 Main Mall, Vancouver, British Columbia, Canada V6T 1Z4 (e-mail: d.pauly@fisheries.ubc.ca)

Fisheries have rarely been 'sustainable'. Rather, fishing has induced serial depletions, long masked by improved technology, geographic expansion and exploitation of previously spurned species lower in the food web. With global catches declining since the late 1980s, continuation of present trends will lead to supply shortfall, for which aquaculture cannot be expected to compensate, and may well exacerbate. Reducing fishing capacity to appropriate levels will require strong reductions of subsidies. Zoning the oceans into unfished marine reserves and areas with limited levels of fishing effort would allow sustainable fisheries, based on resources embedded in functional, diverse ecosystems.

ishing is the catching of aquatic wildlife, the equivalent of hunting bison, deer and rabbits on land. Thus, it is not surprising that industrialscale fishing should generally not be sustainable: industrial-scale hunting, on land, would not be, either. What is surprising rather, is how entrenched the notion is that unspecified 'environmental change' caused, and continues to cause, the collapse of exploited fish populations. Examining the history of fishing and fisheries makes it abundantly clear that humans have had for thousands of years a major impact on target species and their supporting ecosystems<sup>1</sup>. Indeed, the archaeological literature contains many examples of ancient human fishing associated with gradual shifts, through time, to smaller sizes and the serial depletion of species that we now recognize as the symptoms of overfishing<sup>1,2</sup>.

This literature supports the claim that, historically, fisheries have tended to be non-sustainable, although not unexpectedly there is a debate about the cause for this3, and the exceptions<sup>4</sup>. The few uncontested historical examples of sustainable fisheries seem to occur where a superabundance of fish supported small human populations in challenging climates<sup>5</sup>. Sustainability occurred where fish populations were naturally protected by having a large part of their distribution outside of the range of fishing operations. Hence, many large old fecund females, which contribute overwhelmingly to the egg production that renews fish populations, remained untouched. How important such females can be is illustrated by the example of a single ripe female red snapper, Lutjanus campechanus, of 61 cm and 12.5 kg, which contains the same number of eggs (9,300,000) as 212 females of 42 cm and 1.1 kg each<sup>6</sup>. Where such natural protection was absent, that is, where the entire population was accessible to fishing gears, depletion ensued, even if the gear used seems inefficient in retrospect<sup>7,8</sup>. This was usually masked, however, by the availability of other species to target, leading to early instances of depletions observable in the changing size and species composition of fish remains, for example, in middens9.

The fishing process became industrialized in the early nineteenth century when English fishers started operating steam trawlers, soon rendered more effective by power winches and, after the First World War, diesel engines <sup>10</sup>. The

aftermath of the Second World War added another 'peace dividend' to the industrialization of fishing: freezer trawlers, radar and acoustic fish finders. The fleets of the Northern Hemisphere were ready to take on the world.

Fisheries science advanced over this time as well: the two world wars had shown that strongly exploited fish populations, such as those of the North Sea, would recover most, if not all, of their previous abundance when released from fishing<sup>11</sup>. This allowed the construction of models of singlespecies fish populations whose size is affected only by fishing pressure, expressed either as a fishing mortality rate (F, or catch/biomass ratio), or by a measure of fishing effort (f, for example, trawling hours per year) related to F through a catchability coefficient (q): F = qf. Here, q represents the fraction of a population caught by one unit of effort, directly expressing the effectiveness of a gear. Thus, q should be monitored as closely as fishing effort itself, if the impact of fishing on a given stock, as expressed by F, is to be evaluated. Technology changes tend to increase q, leading to increases referred to as 'technology coefficient'14, which quickly renders meaningless any attempts to limit fishing mortality by limiting only fishing effort.

The conclusion of these models, still in use even now (although in greatly modified forms; Box 1), is that adjusting fishing effort to some optimum level should generate 'maximum sustainable' yield, a notion that the fishing industry and the regulatory agencies eagerly adopted — if only in theory<sup>15</sup>. In practice, optimum effort levels were very rarely implemented (the Pacific halibut fishery is one exception<sup>16</sup>). Rather the fisheries expanded their reach, both offshore, by fishing deeper waters and remote sea mounts<sup>17</sup>, and by moving onto the then untapped resources of West Africa<sup>18</sup>, southeast Asia<sup>19</sup>, and other low-latitude and Southern Hemispheric regions<sup>20</sup>.

#### Fisheries go global

In 1950, the newly founded Food and Agriculture Organization (FAO) of the United Nations began collection of global statistics. Fisheries in the early 1950s were at the onset of a period of extremely rapid growth, both in the Northern Hemisphere and along the coast of the countries of what is now known as the developing world. Everywhere that industrial-scale fishing (mainly trawling, but also purse seining

and long-lining) was introduced, it competed with small-scale, or artisanal fisheries. This is especially true for tropical shallow waters (10–100 m), where artisanal fisheries targeting food fish for local consumption, and trawlers targeting shrimps for export, and discarding the associated by-catch, compete for the same resource<sup>21</sup>.

Box :

#### Single-species stock assessments

Single-species assessments have been performed since the early 1950s, when the founders of modern fisheries science<sup>12,13</sup> attempted to equate the concept of sustainability with the notion of optimum fishing mortality, leading to some form of maximum sustainable yield. Most of these models, now much evolved from their original versions (some to baroque complexity, involving hundreds of free parameters), require catch-at-age data. Hence government laboratories, at least in developed countries, spend a large part of their budget on the routine acquisition and interpretation of catch and age-composition data.

Yet, single-species assessment models and the related policies have not served us particularly well, due to at least four broad problems. First, assessment results, although implying limitation on levels of fishing mortality which would have helped maintain stocks if implemented, have often been ignored, on the excuse that they were not 'precise enough' to use as evidence for economically painful restriction of fishing (the 'burden of proof' problem<sup>86</sup>).

Second, the assessment methods have failed badly in a few important cases involving rapid stock declines, and in particular have led us to grossly underestimate the severity of the decline and the increasing ('depensatory') impacts of fishing during the decline<sup>87</sup>.

Third, there has been insufficient attention in some cases to regulatory tactics: the assessments and models have provided reasonable overall targets for management (estimates of long-term sustainable harvest), but we have failed to implement and even develop effective short-term regulatory systems for achieving those targets<sup>88</sup>.

Fourth, we have seen apparently severe violation of the assumptions usually made about 'compensatory responses' in recruitment to reduction in spawning population size. We have usually assumed that decreasing egg production will result in improving juvenile survival (compensation) so that recruitment (eggs × survival) will not fall off rapidly during a stock decline and will hence tend to stop the decline. Some stocks have shown recruitment failure after severe decline, possibly associated with changes in feeding interactions that are becoming known as 'cultivation/depensation' effects<sup>89</sup>. According to this phenomenon, adult predatory fish (such as cod) can control the abundance of potential predators and competitors of their juvenile offspring, but this control lost when these predatory fish become scarce. This may well lead to alternate stable states of ecosystems, which has severe implications for fisheries management<sup>90</sup>.

Jointly, these four broad problems imply a need to complement our single-species assessments by elements drawn from ecology, that is, to move towards ecosystem-based management. What this will consist of is not clearly established, although it is likely that, while retaining single-species models at its core, it will have to explicitly include trophic interaction between species 91, habitat impacts of various gears 50, and a theory for dealing with the optimum placement and size of marine reserves (see main text). Ecosystem-based management will have to rely on the principles of, and lessons learnt from, single-species stock assessments, especially regarding the need to limit fishing mortality. It will certainly not be applicable in areas where effort or catch limits derived from single-species approaches cannot be implemented in the first place.

Throughout the 1950s and 1960s, this huge increase of global fishing effort led to an increase in catches (Fig. 1) so rapid that their trend exceeded human population growth, encouraging an entire generation of managers and politicians to believe that launching more boats would automatically lead to higher catches.

The first collapse with global repercussions was that of the Peruvian anchoveta in 1971–1972, which is often perceived as having been caused by an El Niño event. However, much of the available evidence, including actual catches (about 18 million tonnes²²) exceeding officially reported catches (12 million tonnes), suggest that overfishing was implicated as well. But attributing the collapse of the Peruvian anchoveta to 'environmental effects' allowed business as usual to continue and, in the mid-1970s, this led to the beginning of a decline in total catches from the North Atlantic. The declining trend accelerated in the late 1980s and early 1990s when most of the cod stocks off New England and eastern Canada collapsed, ending fishing traditions reaching back for centuries²³.

Despite these collapses, the global expansion of effort continued<sup>14</sup> and trade in fish products intensified to the extent that they have now become some of the most globalized commodities, whose price increased much faster than the cost of living index<sup>24</sup>. In 1996, FAO published a chronicle of global fisheries showing that a rapidly increasing fraction of world catches originate from stocks that are depleted or collapsed, that is, 'senescent' in FAO's parlance<sup>25</sup>. Yet,

Box 2

#### Trophic levels as indicators of fisheries impacts

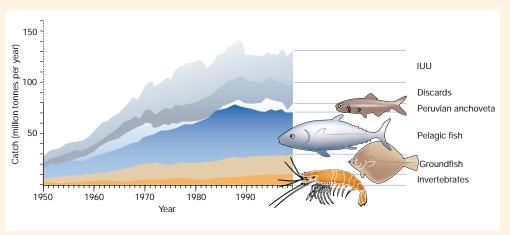
There are many ways ecosystems can be described, for example in terms of the information that is exchanged as their components interact, or in terms of size spectra. But perhaps the most straightforward way to describe ecosystems is in terms of the feeding interactions among their component species, which can be done by studying their stomach contents. A vast historical database of such published studies exists<sup>27</sup>, which has enabled a number of useful generalizations to be made for ecosystem-based management of fisheries. One of these is that marine systems have herbivores (zooplankton) that are usually much smaller than the first-order carnivores (small fishes), which are themselves consumed by much larger piscivorous fishes, and so on. This is a significant difference from terrestrial systems, where, for example, wolves are smaller than the moose they prey on. Another generalization is that the organisms we have so far extracted from marine food webs have tended to play therein roles very different from those played by the terrestrial animals we consume. This can be shown in terms of their 'trophic level' (TL), defined as 1 + the mean TL of their prey.

Thus, in marine systems we have: algae at the bottom of the food web (TL=1, by definition); herbivorous zooplankton feeding on the algae (TL=2); large zooplankton or small fishes, feeding on the herbivorous zooplankton (TL=3); large fishes (for example, cod, tuna and groupers) whose food tends to be a mixture of low- and high-TL organisms (TL=3.5-4.5).

The mean TL of fisheries landings can be used as an index of sustainability in exploited marine ecosystems. Fisheries tend at first to remove large, slower-growing fishes, and thus reduce the mean TL of the fish remaining in an ecosystem. This eventually leads to declining trends of mean TL in the catches extracted from that ecosystem, a process now known as 'fishing down marine food webs'<sup>29</sup>.

Declining TL is an effect that occurs within species as well as between species. Most fishes are hatched as tiny larvae that feed on herbivorous zooplankton. At this stage they have a TL of about 3, but this value increases with size, especially in piscivorous species. Because fisheries tend to reduce the size of the fish in an exploited stock, they also reduce their TL.

Figure 1 Estimated global fish landings 1950–1999. Figures for invertebrates, groundfish, pelagic fish and Peruvian anchoveta are from FAO catch statistics, with adjustment for over-reporting from China<sup>26</sup>. Fish caught but then discarded were not included in the FAO landings; data relate to the early 1990s83 were made proportional to the FAO landings for other periods. Other illegal, unreported or unregulated (IUU) catches<sup>65</sup> were estimated by identifying, for each 5-year block, the dominant jurisdiction and gear use (and hence incentive for IUU)84;



reported catches were then raised by the percentage of IUU in major fisheries for each 5-year block. The resulting estimates of IUU are very tentative (note dotted *y*-axis), and we consider that complementing landings statistics with more reliable estimates of discards and IUU is crucial for a transition to ecosystem-based management.

global catches seemed to continue, increasing through the 1990s according to official catch statistics. This surprising result was explained recently when massive over-reporting of marine fisheries catches by one single country, the People's Republic of China, was uncovered<sup>26</sup>. Correcting for this showed that reported world fisheries landings have in fact been declining slowly since the late 1980s, by about 0.7 million tonnes per year.

#### Fisheries impact on ecosystem and biodiversity

The position within ecosystems of the fishes and invertebrates landed by fisheries can be expressed by their trophic levels, expressing the number of steps they are removed from the algae (occupying a trophic level of 1) that fuel marine food webs (Box 2). Most food fishes have trophic levels ranging from 3.0 to 4.5, that is, from sardines feeding on zooplankton to large cod or tuna feeding on miscellaneous fishes²<sup>7</sup>. Thus, the observed global decline of 0.05–0.10 trophic levels per decade in global fisheries landings (Fig. 2) is extremely worrisome, as it implies the gradual removal of large, long-lived fishes from the ecosystems of the world oceans. This is perhaps most clearly illustrated by a recent study in the North Atlantic showing that the biomass of predatory fishes (with a trophic level of 3.75 or more) declined by two-thirds through the second half to the twentieth century, even though this area was already severely depleted before the start of this time period²<sup>8</sup>.

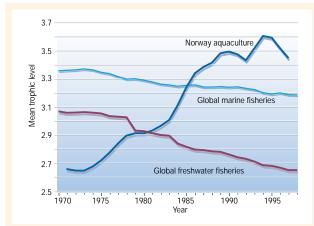
It may be argued that so-called 'fishing down marine food webs' is both a good and an unavoidable thing, given a growing demand for fish<sup>29</sup>. Indeed, the initial ecosystem reaction to the process may be a release from predation, where cascading effects may lead to increased catches<sup>30</sup>. Such effects are, however, seldom observed in marine ecosystems<sup>31,32</sup>, mainly because they do not function simply as a number of unconnected food chains. Rather, predators operate within finely meshed food webs, whose structure (which they help maintain) tends to support the production of their prey. Hence the concept of 'beneficial predation', where a predator may have a direct negative impact on its prey, but also an indirect positive effect, by consuming other predators and competitors of the prey33 (and see Box 1). Thus, removing predators does not necessarily lead to more of their prey becoming available for humans. Instead, it leads to increases or outbursts of previously suppressed species, often invertebrates<sup>30,34,35</sup>, some of which may be exploited (for example, squid or jellyfish, the latter a relatively new resource, exported to east Asia), and some outright noxious<sup>36</sup>.

The principal, direct impact of fishing is that it reduces the abundance of target species. It has often been assumed that this does

not impose any direct threat of species extinction as marine fish generally are very fecund and the ocean expanse is wide<sup>37</sup>. But the past few decades have witnessed a growing awareness that fishes can not only be severely depleted, but also be threatened with extinction through overexploitation<sup>38</sup>. Among commercially important species, those particularly at risk are species that are highly valued, large and slow to mature, have limited geographical range, and/or have sporadic recruitment<sup>39</sup>. There is actually little support, though, for the general assumption that the most highly fecund marine fish species are less susceptible to overexploitation; rather it seems that this perception is flawed<sup>40</sup>. Fisheries may also change the evolutionary characteristics of populations by selectively removing the larger, fast-growing individuals, and one important research question is whether this induces irreversible changes in the gene pool<sup>41</sup>. Overall, this has implications for research, monitoring and management, and it points to the need for incorporating ecological consideration in fisheries management<sup>42,43</sup>, as exemplified by the development of quantitative guidelines to avoid local extinctions<sup>44</sup>.

Another worrisome aspect of fishing down marine food webs is that it involves a reduction of the number and length of pathways linking food fishes to the primary producers, and hence a simplification of the food webs. Diversified food webs allow predators to switch between prey as their abundance fluctuates<sup>45</sup>, and hence to compensate for prey fluctuations induced by environmental fluctuations<sup>46</sup>. Fisheries-induced food-web simplification, combined with the drastic fisheries-induced reduction in the number of year classes in predator populations<sup>47,48</sup>, makes their reduced biomass strongly dependent of annual recruitment. This leads to increasing variability, and to lack of predictability in population sizes, and hence in predicted catches. The net effect is that it will increasingly look like environmental fluctuations impact strongly on fisheries resources, even where they originally did not. This resolves, if in a perverse way, the question of the relative importance of fisheries and environmental variability as the major driver for changes in the abundance of fisheries resources<sup>49</sup> (Fig. 3).

It seems unbelievable in retrospect, but there was a time when it was believed that bottom trawling had little detrimental impact, or even a beneficial impact, on the sea bottom that it 'ploughed'. Recent research shows that the ploughing analogy is inappropriate and that if an analogy is required, it should be that of clear cutting forests in the course of hunting deer. Indeed, the productivity of the benthic organisms at the base of food webs leading to food fishes is seriously impacted by bottom trawling<sup>50</sup>, as is the survival of their juveniles when deprived of the biogenic bottom structure destroyed by that



**Figure 2** Fisheries, both marine and freshwater, are characterized by a decline of the mean trophic level in the landings, implying an increased reliance on organisms low in food webs (data from FishBase<sup>27</sup>, with Peru/Chile excluded owing to the dominance of Peruvian anchoveta; see also Fig. 1). Freshwater fisheries have lower trophic level values overall, indicating an earlier onset of the 'fishing down' phenomenon<sup>29</sup>. The trend is inverted in non-Asian aquaculture, whose production consists increasingly of piscivorous organisms, as illustrated here for Norway (a major producer, yet representative country)<sup>85</sup>.

Exploited population protected by no-take reserves

Exploited population with no reserves

Population crash

Time

**Figure 3** Schematic representation of the effects of some environmental variation on an unexploited, exploited but protected, and exploited but unprotected fish population. This illustrates how protection through a marine reserve (and/or stock rebuilding) can mitigate the effects of environmental fluctuations, including 'regime shifts' (Graph from J. Jackson, personal communication.)

form of fishing<sup>51</sup>. Hence, given the extensive coverage of the world's shelf ecosystems by bottom trawling<sup>52</sup>, it is not surprising that generally longer-lived, demersal (bottom) fishes have tended to decline faster than shorter-lived, pelagic (open water) fishes, a trend also indicated by changes in the ratio of piscivorous (mainly demersal) to zooplanktivorous (mainly pelagic) fishes<sup>53</sup>.

It is difficult to fully appreciate the extent of the changes to ecosystems that fishing has wrought, given shifting baselines as to what is considered a pristine ecosystem<sup>1.54</sup> and continued reliance on single-species models (Box 1). These changes, often involving reductions of commercial fish biomasses to a few per cent of their pre-exploitation levels, prevent us taking much guidance from the concept of sustainability, understood as aiming to maintain what we have<sup>3.8</sup>. Rather, the challenge is rebuilding the stocks in question.

#### Reducing fishing capacity

There is widespread awareness that increases in fishing-fleet capacity represent one of the main threats to the long-term survival of marine capture-fishery resources, and to the fisheries themselves<sup>55,56</sup>. Reasons advanced for the overcapitalization of the world's fisheries include: the open-access nature of many fisheries<sup>57</sup>; common-pool fisheries that are managed non-cooperatively<sup>58,59</sup>; sole-ownership fisheries with high discount rates and/or high price-to-cost ratios<sup>60</sup>; the increasing replacement of small-scale fishing vessels with larger ones<sup>55</sup>; and the payment of subsidies by governments to fishers<sup>61</sup>, which generate 'profits' even when resources are overfished.

This literature shows that fishing overcapacity is likely to build up not only under open access  $^{62}$ , but also under all forms of property regimes. Subsidies, which amount to US\$2.5 billion for the North Atlantic alone, exacerbate the problems arising from the open access and/or 'common pool' aspects of capture fisheries, including fisheries with full-fledged property rights  $^{61.63}$ .

Even subsidies used for vessel decommissioning schemes can have negative effects. In fact, decommissioning schemes can lead to the intended reduction in fleet size only if vessel owners are consistently caught by surprise by those offering this form of subsidy. As this is an unlikely proposition, decommissioning schemes often end up providing the collaterals that banks require to underwrite fleet modernizations. Additionally, in most cases, it is not the actual vessel that

is retired, but its licence. This means that 'retired' vessels can still be used to catch species without quota (so-called 'under-utilized resources', which are often the prey of species for which there is a quota), or deployed along the coast of some developing country, the access to which may also be subsidized<sup>18</sup>. Clearly, the decommissioning schemes that will have to be implemented if we are ever to reduce overcapacity will have to address these deficiencies if they are not to end up, as most have so far, in fleet modernization and increased fishing mortality.

It is clear that a real, drastic reduction of overcapacity will have to occur if fisheries are to acquire some semblance of sustainability. The required reductions will have to be strong enough to reduce F by a factor of two or three in some areas, and even more in others. This must involve even greater decreases in f, because catches can be maintained in the face of dwindling biomasses by increasing q (and hence F; see definitions above), even when nominal effort is constant. Indeed, this is the very reason behind the incessant technological innovation in fisheries, which now relies on global positioning systems and detailed maps of the sea bottom to seek out residual fish concentrations previously protected by rough terrain. This technological race, and the resulting increase in q, is also the reason why fishers often remain unaware of their own impacts on the resource they exploit and object so strongly to scientists' claims of reductions in biomass.

If fleet reduction is done properly, it should result in an increase in net benefits ('rent') from the resources, as predicted by the basic theory of bioeconomics<sup>62</sup>. This can be used, via taxation of the rent gained by the remaining fishers, to ease the transition of those who had to stop fishing. This would contrast with the present situation, where taxes from outside the fisheries sector are used, in form of subsidies, to maintain fishing at levels that are biologically unsustainable, and which ultimately lead to the depletion and collapse of the underlying resources.

#### Biological constraints to fisheries and aquaculture

Perhaps the strongest factor behind the politicians' use of tax money to subsidize non-sustainable, even destructive fisheries, and its tacit support by the public at large, is the notion that, somehow, the oceans will yield what we need — just because we need it. Indeed,

demand projections generated by national and international agencies largely reflect present consumption patterns, which by some means the oceans ought to help us maintain, even if the global human population were to double again. Although much of the deep ocean is indeed unexplored and 'mysterious', we know enough about ocean processes to realize that its productive capacity cannot keep up with an ever-increasing demand for fish.

Just as a tropical scientist might look at the impressive expanse of Canada and assume that this country has boundless potential for agricultural production, unaware that in reality only the thin sliver of land along its southern border (5%) is arable, we terrestrial aliens have assumed that the expanse and depths of the world's oceans will provide for us in the ways that its more familiar coastal fringes have. But this assumption is very wrong. Of the 363 million square kilometres of ocean on this planet, less than 7% — the continental shelves — are shallower than 200 m, and some of this shelf area is covered by ice. Shelves generate the biological production supporting over 90% of global fish catches, the rest consisting of tuna and other oceanic organisms that gather their food from the vast, desert-like expanse of the open oceans.

The overwhelming majority of shelves are now 'sheltered' within the exclusive economic zones (EEZ) of maritime countries, which also include all coral reefs and their fisheries (Box 3). According to the 1982 United Nations Convention on the Law of the Sea<sup>64</sup>, any country that cannot fully utilize the fisheries resource of its EEZ must make this surplus available to the fleet of other countries. This, along with eagerness for foreign exchange, political pressure<sup>18</sup> and illegal fishing<sup>65</sup>, has led to all of the world's shelves being trawled for bottom fish, purse-seined for pelagic fishes and illuminated to attract and catch squid (to the extent that satellites can map the night time location of fishing fleets as well as that of cities). Overall, about 35% of the primary production on the world's shelves is required to sustain the fisheries<sup>66</sup>, a figure similar to the human appropriation of terrestrial primary production<sup>67</sup>.

The constraints to fisheries expansion that this implies, combined with the declining catches alluded to above, have led to suggestions that aquaculture should be able to bridge the gap between supply and demand. Indeed, the impressive recent growth of reported aquaculture is often cited as evidence of the potential of that sector to meet the growing demand for fish, or even to 'feed the world'.

Three lines of argument suggest that this is unlikely. The first is that the rapidly growing global production figures underlying this documented growth are driven to a large extent by the People's Republic of China, which reported 63% of world aquaculture production in 1998. But it is now known that China not only overreports its marine fisheries catches, but also the production of many other sectors of its economy<sup>68</sup>. Thus, there is no reason to believe that global aquaculture production in the past decades has risen as much as officially reported.

Second, modern aquaculture practices are largely unsustainable: they consume natural resources at a high rate and, because of their intensity, they are extremely vulnerable to the pollution and disease outbreaks they induce. Thus, shrimp aquaculture ventures are in many cases operated as slash-and-burn operations, leaving devastated coastal habitats and human communities in their wake <sup>69,70</sup>.

Third, much of what is described as aquaculture, at least in Europe, North America and other parts of the developed world, consists of feedlot operations in which carnivorous fish (mainly salmon, but also various sea bass and other species) are fattened on a diet rich in fish meal and oil. The idea makes commercial sense, as the farmed fish fetch a much higher market price than the fish ground up for fish meal (even though they may consist of species that are consumed by people, such as herring, sardine or mackerels, forming the bulk of the pelagic fishes in Fig. 1). The point is that operations of this type, which are directed to wealthy consumers, use up much more fish flesh than they produce, and hence cannot replace capture fisheries, especially in developing countries, where very few can

Box 3

### Sustainable coral reef fisheries: an oxymoron?

Globally, 75% of coral reefs occur in developing countries where human populations are still increasing rapidly. Although coral reefs account for only 0.1% of the world's ocean, their fisheries resources provide tens of millions of people with food and livelihood<sup>92</sup>. Yet, their food security, as well as other ecosystem functions they provide, is threatened by various human activities, many of which, including forest and land management, are unrelated to fishing<sup>93</sup>.

It has often been assumed that the high levels of primary productivity reported for coral reefs imply high fisheries yields<sup>94</sup>. However, the long-held notion that coral reef fishes are 'fast turnover' species, capable of high productivity, is being increasingly challenged<sup>95</sup>. Yield estimates for coral reefs vary widely, ranging from 0.2 to over 40 tonnes km<sup>-2</sup> yr<sup>-1</sup> (ref. 96), depending on what is defined as coral reef area, and as coral reef fishes<sup>96,97</sup>. Taking yields from the central part of this range (5–15 tonnes km<sup>-2</sup> yr<sup>-1</sup>) and the most comprehensive reef-area estimate available<sup>92</sup>, we derive an estimate for total global annual yield of 1.4–4.2 million tonnes. Although these estimates represent only 2–5% of global fisheries catches, they provide an important, almost irreplaceable, source of animal protein to the populations of many developing countries<sup>96</sup>.

Clearly, maintaining the biodiversity that is a characteristic of healthy reefs is the key to maintaining sustainable reef fisheries. Yet coral reefs throughout the world are being degraded rapidly, especially in developing countries<sup>93</sup>. Concerns regarding overexploitation of reef fisheries are widespread<sup>1,75,98</sup>. The entry of new, non-traditional fishers into reef fisheries has led to intense competition and the use of destructive fishing implements, such as explosives and poisons, a process known as 'malthusian overfishing'<sup>21</sup>.

Another major problem is the growing international trade for live reef fish<sup>99</sup>, often associated with mobile fleets using cyanide fishing, and targeting species that often have limited ranges of movements<sup>100</sup>. This leads to serial depletion of large coral reef fishes, notably the humphead wrasse (*Cheilinus undulatus* Labridae), groupers (Serranidae) and snappers (Lutjanidae), and to reefs devastated by the cyanide applications.

These fisheries, which destroy the habitat of the species upon which they rely, are inherently unsustainable. It can be expected that they will have to cease operating within a few decades, that is, before warm surface waters and sea-level rise overcome what may be left of the world's coral reefs.

afford imported smoked salmon. Indeed, this form of aquaculture represents another source of pressure on wild fish populations<sup>71</sup>.

#### **Perspectives**

We believe the concept of sustainability upon which most quantitative fisheries management is based<sup>72</sup> to be flawed, because there is little point in sustaining stocks whose biomass is but a small fraction of its value at the onset of industrial-scale fishing. Rebuilding of marine systems is needed, and we foresee a practical restoration ecology for the oceans that can take place alongside the extraction of marine resources for human food. Reconciling these apparently dissonant goals provides a major challenge for fisheries ecologists, for the public, for management agencies and for the fishing industry<sup>73</sup>. It is important here to realize that there is no reason to expect marine resources to keep pace with the demand that will result from our growing population, and hopefully, growing incomes in now impoverished parts of the world, although we note that fisheries designed to be sustainable in a world of scarcity may be profitable.

We argued in the beginning of this review that whatever semblance of sustainability fisheries in the past might have had was due

to their inability to cover the entire range inhabited by the wildlife species that were exploited, which thus had natural reserves. We further argued that the models used traditionally to assess fisheries, and to set catch limits, tend to require explicit knowledge on stock status and total withdrawal from stocks, that is, knowledge that will inherently remain imprecise and error prone. We also showed that generally overcapitalized fisheries are leading, globally, to the gradual elimination of large, long-lived fishes from marine ecosystems, and their replacement by shorter-lived fishes and invertebrates, operating within food webs that are much simplified and lack their former 'buffering' capacity.

If these trends are to be reversed, a huge reduction of fishing effort involving effective decommissioning of a large fraction of the world's fishing fleet will have to be implemented, along with fisheries regulations incorporating a strong form of the precautionary principle. The conceptual elements required for this are in place, for example, in form of the FAO Code of Conduct for Responsible Fisheries<sup>74</sup>, but the required political will has been lacking so far, an absence that is becoming more glaring as increasing numbers of fisheries collapse throughout the world, and catches continue to

Given the high level of uncertainty facing the management of fisheries, which induced several collapses, it has been suggested by numerous authors that closing a part of the fishing grounds would prevent overexploitation by setting an upper limit on fishing mortality. Marine protected areas (MPAs), with no-take reserves at their core, combined with a strongly limited effort in the remaining fishable areas, have been shown to have positive effects in helping to rebuild depleted stocks75-77. In most cases, the successful MPAs were used to protect rather sedentary species, rebuild their biomass, and eventually sustain the fishery outside the reserves by exporting juveniles or adults<sup>75</sup>. Although migrating species would not benefit from the local reduction in fishing mortality caused by an MPA<sup>78,79</sup>, the MPA would still help some of these species by rebuilding the complexity of their habitat destroyed by trawling, and thus decrease mortality of their juveniles<sup>80</sup>. Enforcement of the no-take zones within MPAs would benefit from the application of high technology (for example, satellite monitoring of fishing vessels), presently used mainly to increase fishing pressure.

There is still much fear among fisheries scientists, especially in extra-tropical areas, that the export of fish from such reserves would not be sufficient to compensate for the loss of fishing ground<sup>81</sup>. Although we agree that marine reserves are no panacea, the present trends in fisheries, combined with the low degree of protection presently afforded (only 0.01% of the world's ocean is effectively protected), virtually guarantee that more fish stocks will collapse, and that these collapses will be attributed to environmental fluctuations or climate change (Fig. 3). Moreover, many exploited fish populations and eventually fish species will become extinct. MPAs that cover a representative set of marine habitats should help prevent this, just like forest and other natural terrestrial habitats have enabled the survival of wildlife species which agriculture would have otherwise rendered extinct.

Focused studies on the appropriate size and location of marine reserves and their combination into networks, given locale-specific oceanographic conditions, should therefore be supported. This will lead to the identification of reserve designs that would optimize export to adjacent fished areas, and which could thus be offered to the affected coastal and fisher communities, whose consent and support will be required to establish marine reserves and restructure the fisheries8. The general public could also be involved, through eco-labelling and other market-driven schemes, and through support for conservation-orientated non-government organizations, which can complement the activities of governmental regulatory

In conclusion, we think that the restoration of marine ecosystems to some state that existed in the past is a logical policy

goal<sup>82</sup>. There is still time to achieve this, and for our fisheries to be put on a path towards sustainability.

#### doi:10.1038/nature01017

- 1. Jackson, J. B. C. et al. Historical overfishing and the recent collapse of coastal ecosystems. Science 293,
- Orensanz, J. M. L., Armstrong, J., Armstrong, D. & Hilborn, R. Crustacean resources are vulnerable to serial depletion—the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. Rev. Fish Biol. Fish. 8, 117-176 (1998)
- Ludwig, D., Hilborn, R. & Walters, C. Uncertainty, resource exploitation, and conservation: Lessons from history. Science 260, 17-18 (1993).
- 4. Rosenberg, A. A., Fogarty, M. J., Sissenwine, M. P., Beddington, J. R. & Shepherd, J. G. Achieving sustainable use of renewable resources. Science 262, 828-829 (1993).
- Boyd, R. T. in Handbook of American Indians: Northwest Coast (ed. Suttles, W.) 135-148 (Smithsonian Institute, Washington DC, 1990).
- 6. Bohnsack, J. A. (Subcommittee Chair) NOAA Tech. Memo. NMFS-SEFC-261 (National Oceanic and Atmospheric Agency, Miami, 1990).
- Yellen, J. E., Brooks, A. S., Cornelissen, E., Mehlman, M. J. & Stewart, K. A middle stone-age worked bone industry from Katanda, Upper Semliki Valley, Zaire. Science  ${\bf 268}, 553-556 \ (1995)$
- $8. \ \ Pitcher, T.\,J.\,Fisheries\,managed\,to\,rebuild\,ecosystems?\,Reconstructing\,the\,past\,to\,salvage\,the\,future.$ Ecol. Applic. 11, 601-617 (2001).
- 9. Wing, E. S. The sustainability of resources used by native Americans on four Caribbean islands. Int. J. Osteoarchaeol. 11, 112-126 (2001).
- 10. Cushing, D. H. The Provident Sea (Cambridge Univ. Press, Cambridge, 1987).
- 11. Hardy, A. The Open Sea (Collins, London, 1956).
- $12. Schaefer, M.\ B.\ Some\ aspects\ of\ the\ dynamics\ of\ populations\ important\ to\ the\ management\ of\ the$ commercial marine fisheries. Bull. Inter-Am. Trop. Tuna Commiss. 1, 27-56 (1954).
- 13. Beverton, R. J. H. & Holt, S. J. On the Dynamics of Exploited Fish Populations (Chapman and Hall. London, 1957; Facsimile reprint 1993).
- 14. Garcia, S. M. & Newton, C. in Global Trends: Fisheries Management (ed. Sissenwine, M. P.) Am. Fish. Soc. Symp. 20, 3-27 (American Fisheries Society, Bethesda, MD, 1997).
- 15. Mace, P. M. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. Fish Fish. 2, 2-32 (2001).
- 16. Clark, W. G., Hare, S. R., Parma, A. M., Sullivan, P. J. & Trumble, R. J. Decadal changes in growth and recruitment of Pacific halibut (Hippoglossus stenolepis). Can. J. Fish. Aquat. Sci. 56, 242-252 (1999).
- 17. Koslow, J. A. et al. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. ICES J. Mar. Sci. 57, 548-557 (1999).
- 18. Kaczynski, V. M. & Fluharty, D. L. European policies in West Africa: who benefits from fisheries agreements, Mar. Policy 26, 75-93 (2002).
- 19. Silvestre, G. & Pauly, D. Status and Management of Tropical Coastal Fisheries in Asia (ICLARM, Makati City, Philippines, 1997).
- 20. Thorpe, A. & Bennett, E. Globalisation and the sustainability of world fisheries: a view from Latin America. Mar. Resource Econ. 16, 143-164 (2001)
- 21. Pauly, D. Small-scale Fisheries in the Tropics: Marginality, Marginalization, and Some Implications for Fisheries Management (eds Pikitch, E. K., Huppert, D. D. & Sissenwine, M. P.) (American Fisheries Society, Bethesda, MD, 1997)
- 22. Castillo, S. & Mendo, J. in The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change (eds Pauly, D. & Tsukayama, I.) ICLARM Stud. Rev. 15, 109-116 (ICLARM, Manila, Philippines, 1987).
- 23. Myers, R. A., Hutchings, J. A. & Barrowman, N. J. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecol. Applic. 7, 91-106 (1997).
- 24. Sumaila, U. R. in Proc. Expo '98 Conf. Ocean Food Webs Econ. Product., Lisbon, 1-3 July 1998 (eds Pauly, D., Christensen, V. & Coelho, L.) ACP-EU Fish. Res. Rep. 5, 87 (ACP-EU, Brussels, 1999).
- 25. Grainger, R. J. R. & Garcia, S. M. Chronicles of Marine Fishery Landings (1950-1994). Trend Analysis and Fisheries Potential FAO Fish. Tech. Pap. 359 (Food and Agriculture Organization of the United Nations, Rome, 1996).
- Watson, R. & Pauly, D. Systematic distortions in world fisheries catch trends. Nature 424, 534

  –536 (2001).
- 27. Froese, R. & Pauly, D. (eds) FishBase 2000: Concepts, Design and Data Sources (distributed with four CD-ROMs; updates available at http://www.fishbase.org) (ICLARM, Los Baños, Philippines, 2000).
- 28. Christensen, V. et al. in Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses (eds Guénette, S., Christensen, V. & Pauly, D.) Fisheries Centre Res. Rep. 9(4), 1-25 (also available at http://www.fisheries.ubc.ca) (Fisheries Centre, Univ. British Columbia, Vancouver, 2002).
- 29. Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. Jr Fishing down marine food webs. Science 279, 860-863 (1998).
- 30. Daskalov, G. M. Overfishing drives a trophic cascade in the Black Sea. Mar. Ecol. Prog. Ser. 225, 53-63
- 31. Pace, M. L., Cole, J. J., Carpenter, S. R. & Kitchell, J. F. Trophic cascades revealed in diverse ecosystems. Trends Ecol. Evol. 14, 483-488 (1999).
- 32. Pinnegar, J. K. et al. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environ. Conserv. 27, 179-200 (2000).
- 33. Ulanowicz, R. E. & Puccia, C. J. Mixed trophic impacts in ecosystems. Coenoses 5, 7–16. (1990).
- 34. Parsons, T. R. in Food Webs: Integration of Patterns and Dynamics (eds Polis, G. A. & Winemiller, K. D.) 352-357 (Chapman and Hall, New York, 1996)
- $35. \,Mills, C.\,E.\,Jelly fish\,blooms; are populations increasing globally\,in\,response\,to\,changing\,ocean$ conditions? Hydrobiologia 451, 55-68 (2001).
- 36. Van Dolah, F. M., Roelke, D. & Greene, R. M. Health and ecological impacts of harmful algal blooms: risk assessment needs. Hum. Ecol. Risk Assess. 7, 1329-1345 (2001). 37. Pitcher, T. J. A cover story: fisheries may drive stocks to extinction. Rev. Fish Biol. Fish. 8, 367-370 (1998).
- 38. Casey, J. M. & Myers, R. A. Near extinction of a large, widely distributed fish. Science 281, 690-692 (1998).
- $39. Sadovy, Y. The threat of fishing to highly fecund fishes. {\it J. Fish Biol.} ~\bf 59, 90-108~(2001).$ 40. Hutchings, J. A. Collapse and recovery of marine fishes. Nature 406, 882-885 (2000).
- 41. Law, R. Fishing, selection, and phenotypic evolution. ICES J. Mar. Sci. 57, 659-668 (2000).
- 42. Gislason, H., Sinclair, M., Sainsbury, K. & O'Boyle, R. Symposium overview: incorporating ecosystem objectives within fisheries management. Ices J. Mar. Sci. 57, 468-475 (2000).

- 43. Hutchings, J. A. Numerical assessment in the front seat, ecology and evolution in the back seat: Time to change drivers in fisheries and aquatic sciences? Mar. Ecol. Prog. Ser. 208, 299–313 (2000).
- 44. Punt, A. E. Extinction of marine renewable resources: a demographic analysis. *Popul. Ecol.* 42, 19–27 (2000).
- 45. Stephens, D. W. & Krebs, J. R. Foraging Theory (Princeton Univ. Press, Princeton, 1986).
- Neutel, A.-M., Heesterbeek, J. A. P. & de Ruiter, P. C. Stability in real food webs: weak links in long loops. Science 296, 1120–1123 (2002).
- 47. Longhurst, A. Cod: perhaps if we all stood back a bit? Fish. Res. 38, 101-108 (1998).
- Stergiou, K. I. Overfishing, tropicalization of fish stocks, uncertainty and ecosystem management: resharpening Ockham's razor. Fish. Res. 55, 1–9 (2002).
- $49. \, Steele, J. \, H. \, Regime \, shifts \, in \, marine \, ecosystems. \, \textit{Ecol. Applic.} \, \textbf{8} (Suppl. \, 1), S33-S36 \, (1998).$
- 50. Hall, S. J. The Effects of Fisheries on Ecosystems and Communities (Blackwell, Oxford, 1998).
- Turner, S. J., Thrush, S. F., Hewitt, J. E., Cummings, V. J. & Funnell, G. Fishing impacts and the degradation or loss of habitat structure. Fish. Mgmt Ecol. 6, 401–420 (1999).
- Watling, L. & Norse, E. A. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. Conserv. Biol. 12, 1180–1197 (1998).
- 53. Caddy, J. F. & Garibaldi, L. Apparent changes in the trophic composition of world marine harvests: the perspective from the FAO capture database. *Ocean Coastal Mgmt* 43, 615–655 (2000).
- 54. Pauly, D. Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol. Evol.* **10**, 430 (1995).
- Weber, P. Facing limits to oceanic fisheries: Part II: The social consequences. Nat. Res. Forum 19, 39–46 (1995)
- 56. Mace, P. M. in Developing and Sustaining World Fisheries Resources (Proc. 2nd World Fish. Congr.) (eds Hancock, D. H., Smith, D. C. & Beumer, J.) 1–20 (CSIRO Publishing, Collingwood, VIC, 1997).
- Gordon, H. S. The economic theory of a common property resource: the fishery. J. Polit. Econ. 62, 124–142 (1954).
- Munro, G. The optimal management of transboundary renewable resources. Can. J. Econ. 12, 355–376 (1979).
- Sumaila, U. R. Cooperative and non-cooperative exploitation of the Arcto-Norwegian cod stock in the Barents Sea. Environ. Resource Econ. 10, 147–165 (1997).
- 60. Sumaila, U. R. & Bawumia, M. in Fish Ethics: Justice in the Canadian Fisheries (eds Coward, H., Ommer, R. & Pitcher, T. J.) 140–153. (Institute of Social and Economic Research, Memorial University, St John's, Newfoundland, 2000).
- 61. Munro, G. R. & Sumaila, U. R. in Fisheries Centre Research Report 9(5) (eds Pitcher, T. J., Sumaila, U. R. & Pauly, D.) 10–27 (also available at http://www.fisheries.ubc.ca) (Fisheries Centre, Univ. British Columbia, Vancouver, 2001).
- Clark, C. W. Mathematical Bioeconomics: The Optimal Management of Renewable Resources (Wiley, New York, 1990).
- 63. Milazzo, M. World Bank Tech. Pap. No. 406 (World Bank, Washington DC, 1998).
- 64. United Nations. The United Nations Convention on the Law of the Sea (United Nations, New York, 1982).
- $65.\,Bray,\,K.\,FAO\,Rep.\,IUU/2000/6,\,53$  (Food and Agriculture Organization of the United Nations, Rome, 2000).
- Pauly, D. & Christensen, V. Primary production required to sustain global fisheries. Nature 374, 255–257 (1995).
- 67. Vitousek, P. M., Ehrlich, P. R. & Ehrlich, A. H. Human appropriation of the products of photosynthesis. *BioScience* 36, 368–373 (1986).
- Rawski, T. G. & Xiao, W. Roundtable on Chinese economic statistics: introduction. China Econ. Rev. 12, 298–302 (2001).
- Feigon, L. A harbinger of the problems confronting China's economy and environment: the great Chinese shrimp disaster of 1993. J. Contemp. China 9, 323–332 (2000).
- Pullin, R. S. V., Rosenthal, H. & Maclean, J. L. (eds) Environment and Aquaculture in Developing Countries (ICLARM, Manila, Philippines, 1993).
- 71. Naylor, R. L. et al. Effect of aquaculture on world fish supplies. Nature 405, 1017–1024 (2000).
- Sainsbury, K. J., Punt, A. E. & Smith, A. D. M. Design of operational management strategies for achieving fishery ecosystem objectives. *Ices J. Mar. Sci.* 57, 731–741 (2000).
- $73. Cochrane, K.\ L.\ Reconciling sustainability, economic efficiency and equity in fisheries: the one that got away? \textit{Fish Fish.}\ 1,3–21 (2000).$
- 74. Edeson, W. R. Current legal development. The Code of Conduct for Responsible Fisheries: an introduction. Int. J. Mar. Coast. Law 11, 233–238 (1996).
- Roberts, C. M., Bohnsack, J. A., Gell, F., Hawkins, J. P. & Goodridge, R. Effects of marine reserves on adjacent fisheries. Science 294, 1920–1923 (2001).

- Mosquera, I., Côté, I. M., Jennings, S. & Reynolds, J. D. Conservation benefits of marine reserves for fish populations. *Anim. Conserv.* 3, 321–332 (2000).
- 77. Murawski, S. A., Brown, R., Lai, H. L., Rago, P. R. & Hendrickson, L. Large-scale closed areas as a fishery management tool in temperate marine systems: the Georges Bank experience. *Bull. Mar. Sci.* 66, 775–798 (2000).
- Guénette, S., Pitcher, T. J. & Walters, C. J. The potential of marine reserves for the management of northern cod in Newfoundland. *Bull. Mar. Sci.* 66, 831–852 (2000).
- Lipcius, R. N., Seitz, R. D., Goldsborough, W. J., Montane, M. M. & Stockhausen, W. T. in Spatial Processes and Management of Marine Populations (ed. Witherell, D.) 643–666 (Alaska Sea Grant College Program, Anchorage, 2001).
- Lindholm, J. B. I., Auster, P. J. & Kaufman, L. Habitat-mediated survivorship of 0-year Atlantic cod (Gadus morhua). Mar. Ecol. Prog. Ser. 180, 247–255 (1999).
- 81. Tupper, M. K. et al. Marine reserves and fisheries management. Science 295, 1233-1235 (2002).
- Sumaila, U. R., Pitcher, T. J., Haggan, N. & Jones, R. in Microbehavior and Macroresults: Proc. 10th Biannual Conf. Int. Inst. Fish. Econ. Trade, Corvallis, Oregon, 10-14 July 2000 (eds Johnston, R. S. & Shriver, A. L.) (International Institute of Fisheries Economics & Trade, Corvallis, OR, 2001).
- Alverson, D. L., Freeberg, M. H., Murawski, S. A. & Pope, J. G. FAO Fish. Tech. Pap. 339, 233 (Food and Agriculture Organization of the United Nations, Rome, 1994).
- 84. Forrest, R., Pitcher, T., Watson, R., Valtýsson, H. & Guénette, S. in Fisheries Impacts on North Atlantic Ecosystems: Evaluations and Policy Exploration (ed. Pauly, D.) Fisheries Centre Rep. 5, 81–93 (also available at http://www.fisheries.ubc.ca) (Fisheries Centre, Univ. British Columbia, Vancouver, 2001).
- Pauly, D., Tyedmers, P., Froese, R. & Liu, L. Y. Fishing down and farming up the food web. Conserv Biol. Pract. 2, 25 (2001).
- Dayton, P. K. Ecology—reversal of the burden of proof in fisheries management. Science 279, 821–822 (1998).
- Walters, C. J. & Maguire, J. J. Lessons for stock assessment from the Northern Cod collapse. Rev. Fish Biol. Fish. 6, 125–137 (1996).
- Perry, R. I., Walters, C. J. & Boutillier, J. A. A framework for providing scientific advice for the management of new and developing invertebrate fisheries. Rev. Fish Biol. Fish. 9, 125–150 (1999).
- Walters, C. & Kitchell, J. F. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Can. J. Fish. Aquat. Sci. 58, 39–50 (2001).
- Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. & Walker, B. Catastrophic shifts in ecosystems. Nature 413, 591–596 (2001).
- 91. Walters, C., Pauly, D., Christensen, V. & Kitchell, J. F. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. *Ecosystems* 3, 70–83 (2000).
- Spalding, M. D., Ravilious, C. & Green, E. P. World Atlas of Coral Reefs (Univ. California Press, Berkeley, 2001).
- Roberts, C. M. et al. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295, 1280–1284 (2002).
- 94. Lewis, J. B. Processes of organic production on coral reefs. Biol. Rev. Cambr. Phil. Soc. 52, 305-347 (1977).
- Choat, J. H. & Robertson, D. R. in Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem (ed. Sale, P. F.) 57–80 (Academic, San Diego, 2002).
- 96. Russ, G. R. in *The Ecology of Fishes on Coral Reefs* (ed. Sale, P. F.) 601–635 (Academic, San Diego, 1991). 97. Spalding, M. D. & Grenfell, A. M. New estimates of global and regional coral reef areas. *Coral Reefs* 16, 225–230 (1997).
- 98. Russ, G. R. in Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem (ed. Sale, P. F.) 421–443 (Academic, San Diego, 2002).
- Sadovy, Y. J. & Vincent, A. C. J. in Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem (ed. Sale, P. F.) 391–420 (Academic, San Diego, 2002).
- 100.Zeller, D. C. Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). Mar. Ecol. Prog. Ser. 154, 65–77 (1997).

#### Acknowledgements

The work forms part of the Sea Around Us project at the Fisheries Centre, University of British Columbia, an activity initiated and funded by the Pew Charitable Trusts. D.P. and C.W. also acknowledge support from the Canadian National Scientific and Engineering Research Council. We thank G. Russ and M. L. 'Deng' Palomares for various suggestions that improved an earlier draft of our paper.