

## Some Ecological, Experimental and Evolutionary Aspects of the Upwelling Ecosystem

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### Introduction

In recent years the upwelling ecosystem has received the close attention of many researchers.<sup>1,2</sup> If we describe this ecosystem as being the result of a divergent water mass, then by contrast a different ecology from that of an upwelling ecosystem should be found in a convergent water mass. These two extremes in marine communities can be seen to occur on a global scale (Fig. 1). The upwelling ecosystem is a general but not exclusive characteristic of western seaboard, such as the Peru, Benguela and Canary Currents, while the convergent ecosystem is generally (but again, not exclusively) found on eastern seaboard, such as in the Caribbean and off the east coast of Australia. Biologically, the former is characterized by coelenterate ecology, including both the corals (Anthozoa) and true jellyfish (Scyphozoa). Far less attention has been given to the ecology of the convergent ecosystem because of its limited commercial importance to man. In particular, while the presence of corals is very apparent in the coastal portions of these areas, the presence of jellyfish as dominant tertiary predators is less well-documented except where they interfere with holidaymakers, such as in the case of the blue bottle, *Physalia physalis*, and box jelly, *Chironex fleckeri*, in Australian waters.<sup>3</sup> In addition the role of gelatinous zooplankton in the ecology of the Sargasso Sea has been appreciated recently through direct observation by SCUBA divers.<sup>4</sup>

In this article an attempt is made to contrast the upwelling ecosystem with its convergent counterpart. This will be done using ecological, experimental and evolutionary evidence in order to understand how these two different systems compete for dominance in different parts of the oceans.

### Ecological considerations

In Fig. 2 the primary productivities of different pelagic ecosystems have been compared in terms of two forms of energy. While radiant energy is easily understood and quantified, the term 'exometabolic energy' comes from Margalef<sup>5</sup> and represents external energy which does not go through the photosynthetic pathway; this is energy made available to the ecosystem as a result of interac-

tions between the atmosphere and hydrosphere, the two most important forms being turbulence and advection.

In Fig. 2 it can be seen that the highest primary production is found in coastal areas where rivers and tidal exchange cause a continual input of exometabolic energy. Such systems generate much higher seaweed production than phytoplankton production. However, in the upwelling ecosystem where no surface is available for macrophyte production, food chains based on phytoplankton eventually lead to the more useful production of fish for man. In cases where too much turbulence exists, primary productivity is suppressed, such as during the winter months in temperate latitudes. Finally, the lowest primary productivities are found in highly stable water masses, such as the Sargasso Sea or in the Hudson Bay where the input of both exometabolic energy and radiant energy is low for appreciable parts of the year. As an anticyclonic gyre, the Sargasso Sea has no upwelling component but tends instead towards a conservation of water within the centre of the gyre. This represents an entirely pelagic form of the convergent ecosystem.

Differences in the ecologies of the ecosystems represented in Fig. 2 are more marked than can be represented by primary production alone. Thus the upwelling ecosystem is generally characterized by the growth of large, long-chain diatoms,<sup>6</sup> whereas the contrasting convergent ecosystem is characterized by the growth of flagellates.<sup>7</sup> These differences in the type of primary producer are not limited to geographically contrasting water masses but occur also as a temporal change and in contiguous ocean waters. Margalef<sup>8</sup> has described the former as a progression from a low diversity, highly productive ecosystem which matures in time to one of high diversity and low production. In a temperate coastal environment, such changes have been documented as starting with a diatom bloom in spring accompanied by the production of large copepods and the arrival of many species of fish; later in the summer, the system develops into a flagellate ecology with the production of smaller copepods and large numbers of ctenophores and jellyfish.<sup>9</sup> Timonin<sup>10</sup> has referred to the same processes in contiguous bodies of water in the Indian Ocean. In his description, the ecology of

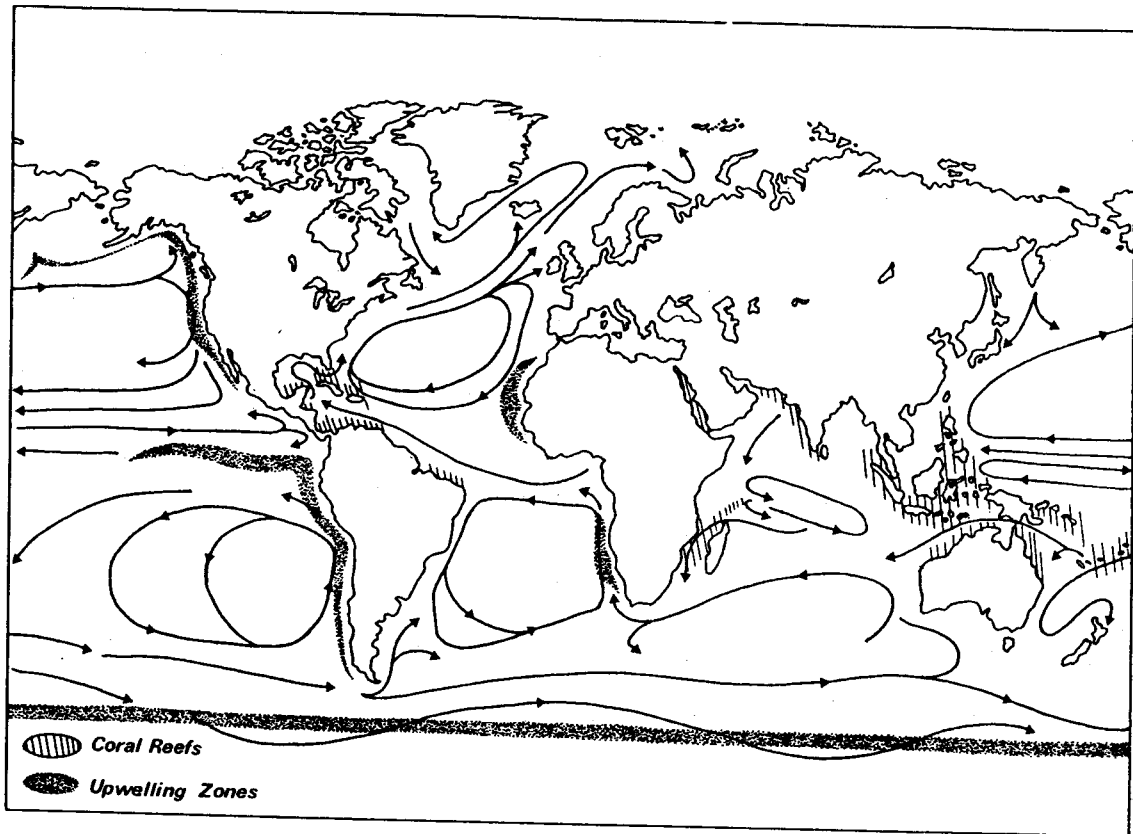


Fig. 1. The approximate distribution of upwelling areas<sup>27</sup> and coral reefs<sup>28</sup> in the hydrosphere.

divergent waters was characterized by coarse herbivorous feeders, including euphausiids, while in stable stratified waters the zooplankton were represented by smaller species of fine filter feeders.

Thus from ecological considerations of the two contrasting ecosystems, a difference emerges, not only in the total amount of primary productivity but also in the food chain established by a diatom-dominated ecology in the upwelling ecosystem and the predominance of small flagellates in the convergent system. In order to understand how the food chains of these two communities function, it is necessary to examine the results of some recent experiments.

**Experimental considerations**

The basic question of why diatoms should dominate in upwelling systems and small flagellates in convergent ones can be examined in the light of recent experiments by Turpin and Harrison.<sup>11</sup> One result is shown in Fig. 3, where a division of diatom versus flagellate dominance was obtained by varying the flux of a specific nutrient, such as occurs naturally under the two extremes of stable and turbulent conditions. Further unpublished data indicate that the patchiness of the limiting nutrient may play a role in the control of cell size. Their data show that with low frequency pulsing of the nutrient, large, long-chained centric diatoms dominated.<sup>12</sup> In contrast, flagellates assumed the greatest importance under conditions of a low nutrient availability. Stated in terms of nutrient uptake kinetics, this can be explained by the large centrate diatoms having a high  $V_{max}$  for the uptake of a nutrient, while flagellates reach an optimum in a low nutrient environment by having an increased substrate affinity. In addition, it is suggested that the lower specific rate of respiration for large cells compared with small cells will allow the former to out-compete the latter under conditions of a pulsed nutrient supply which requires cells to take up nutrients rapidly when they are available, but survive on their metabolic reserves when they are not.

The fact that diatoms can out-compete flagellates in their

maximum growth rates has been documented by several researchers.<sup>13,14</sup> In these experiments it was shown that under favourable conditions the Bacillariophyceae generally have a much higher growth rate than all other classes of algae, including the dinoflagellates. In field studies it has further been observed that diatoms dominate under spring bloom conditions of high nutrient availability and turbulence.<sup>15,16</sup>

Having established the dominance of diatom communities in the high exometabolic energy environment of upwelled ecosystems, it is necessary to consider the trophic consequences of the food chain established as a result of their presence. This subject has recently been reviewed by Greve and Parsons<sup>17</sup> who suggested, largely as the result of experimental work, that two contemporary food chains could be identified, based on either diatom or flagellate ecology, as follows:

diatoms → large zooplankton → fish

flagellates → small zooplankton → jellyfish

The essential difference at the tertiary level of production was in the

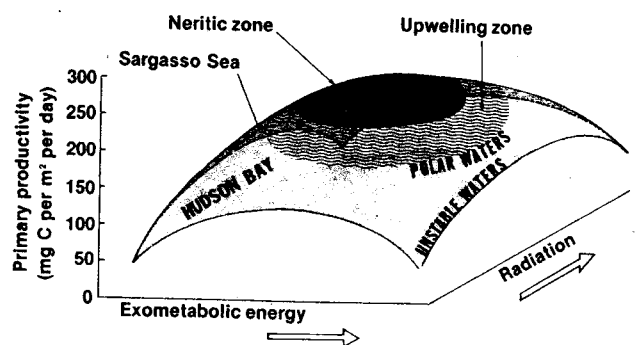


Fig. 2. Primary productivities of different ocean areas represented as a continuum in terms of differences in exometabolic and radiant energy.

form of predation; being raptorial sight feeders, fish have a tendency to select large prey in order to reduce the energy cost of gathering many small prey, whereas jellyfish (including both medusae and ctenophores) have a non-specific tendency to collect small food items because large prey are difficult to retain and may even break the tentacles of their filtering apparatus. When one considers marine mammals, a further point (which was not suggested at the time in the above reference) is that whales not only have the advantage of touch and sight as in the case of jellyfish and fish respectively, but they have the further benefit of being able to use some form of sonar to detect large concentrations of prey. This is a significant advantage in a highly productive but patchy environment, such as is found in upwelling ecosystems.

In addition to the energy advantage gained by raptorial feeding on large particles as described above, the absolute length of the food chain also governs how much energy is delivered to the top trophic position. This has been described by Ryther,<sup>18</sup> who showed that long food chains lost much more energy than short food chains. Since long food chains are the result of the primary producers being very small, it is postulated that it is both the difficulty of capturing small food particles by raptorial feeding and the low energetics of such food chains which forces the ecology into a low energy, coelenterate ecosystem.

### Evolutionary considerations

In the following discussion an attempt is made to offer an evolutionary explanation for differences in the trophic structure of the sea, leading up to the biology of the highly productive upwelling ecosystem. Evidence offered in this respect is taken largely from the fossil record but the explanation of how the different systems function relies on a knowledge of the energy requirements of top predators, as well as on some of the ecological and experimental evidence discussed above.

The three top predators in the sea in terms of the order in which they evolved are the jellyfish, the fish and the whales. (Other leading predators which will not be considered here are cephalopods, reptiles and birds.) From Fenchel<sup>19</sup> it is apparent that the mass-specific energy requirements of primitive organisms, heterotherms and homiotherms increase by two orders of magnitude. Thus, it is approximately 30 times more metabolically costly to be a whale per unit mass of tissue than a heterotherm, such as a fish. It is approximately 7 times more costly to be a heterotherm than a protozoan, all masses being hypothetically equal. Assuming that the jellyfish has a mass-specific metabolism similar to large protozoa,\* the question which may be asked is, where did the extra energy come from in order to support the greatly increased metabolic needs of the more highly evolved predators of the sea? In terrestrial ecology this is analogous to asking why the Serengeti Plain in Africa can support so many lions. The answer requires a review of the main features of the fossil record as it pertains to the energetics of pelagic ecosystems.

An approximate summary of the emergence of different forms of life in the oceans is shown in Fig. 3. From an evolutionary point of view it is generally believed<sup>21,22</sup> that the early pelagic environment of the oceans contained small green, blue-green and red algae, at least from Precambrian times to the beginning of the Devonian when the first dinoflagellates appeared in any abundance. During the period beginning with the lower Cambrian, fossil records indicate that the dominant pelagic predators were the Coelenterates, including Hydrozoa and Scyphozoa; the Anthozoa, or corals, started somewhat later in the Ordovician.<sup>23</sup> All these classes of organisms have equivalent species which are present in the ocean today. What provided the missing step in the food chain between primary producers and the carnivorous Coelenterates can only be

\*It may be shown<sup>20</sup> that a ctenophore, *Mnemiopsis leidyi*, has a log specific metabolism of  $-4.06$  for a log weight of  $0.69$ . These values would place the ctenophore on an extension of Fenchel's protozoan curve.

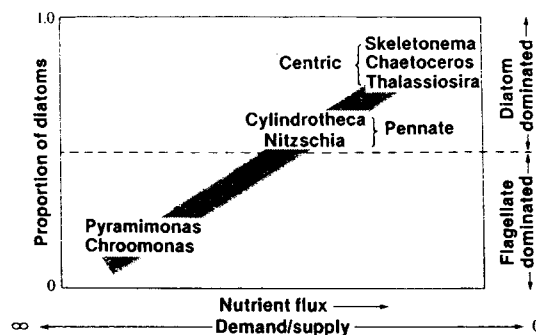


Fig. 3. A schematic representation of the possible relationship between specific nutrient flux (nitrogen) and phytoplankton community structure. Figure results were obtained from chemostat studies and a modified presentation from Turpin and Harrison.<sup>11</sup>

guessed, since the large herbivorous crustacean community which forms most of the secondary production in recent oceans was not present in the period from approximately 500 to 250 million years ago. However, plentiful records exist of protozoans and ostracods in the lower Cambrian<sup>21,23</sup> and since these animals are largely herbivorous feeders they could have been among the filter-feeding plankton which filled the step between the primary and tertiary producers in the ancient pelagic ecosystem.

Although the first fish appeared in the Silurian, their feeding habits appear to have been largely benthic and it is the Devonian which is generally heralded as the start of the Age of Fishes. At this point, part of the predatory pattern of the pelagic environment changed from the non-specific filter-feeding of the carnivorous Coelenterates to the much more metabolically costly feeding of the raptorial fishes. The question is, how was this change in the trophic structure of the sea accomplished?

From the suggestion<sup>17</sup> that raptorial feeders select for larger prey organisms, it is necessary to assume that these were made available through a fundamental change in the size spectrum of primary producers. A further corollary is to assume that this change was made in a way which also increased the total energy available in the ocean, in order to support the energy cost of a nekton community, both because of its higher metabolic rate than that of more primitive organisms<sup>19</sup> and because nekton require additional energy to pursue their prey actively by swimming. This change could have been brought about by the evolution of the dinoflagellates, a development which appears to have occurred at approximately the same time in the early Devonian.<sup>21,22</sup> Representatives of this class of algae can have cell sizes several orders of magnitude larger than most of the planktonic red, green or blue-green algae found in pelagic regions. However, an increase in cell size was not the only advantage offered by this new class of pelagic algae; they also possessed accessory pigments (chlorophyll *c* and peridinin) which efficiently absorbed light in the blue region of the spectrum.<sup>24</sup>

The red, green and blue-green algae do not possess such pigments as efficient at gathering light for photosynthesis in this part of the spectrum. Since the dominant wavelength of light in the marine euphotic zone below the first few metres is in the vicinity of 450 nm, it is deduced that the appearance of the dinoflagellates resulted not only in a larger prey size for secondary producers but also in a much higher total primary production due to the utilization of more light at depth in the oceans.

Also during the Devonian, it has been suggested that radiations occurred in the pelagic crustaceans, leading eventually to the large herbivorous crustacean community that is found in the oceans today.<sup>25</sup> However, the essential abundance of these organisms was not simply due to an increase in the size of primary producers resulting from the appearance of larger flagellates. In more recent times, starting about 100 million years ago in the Cretaceous, it was

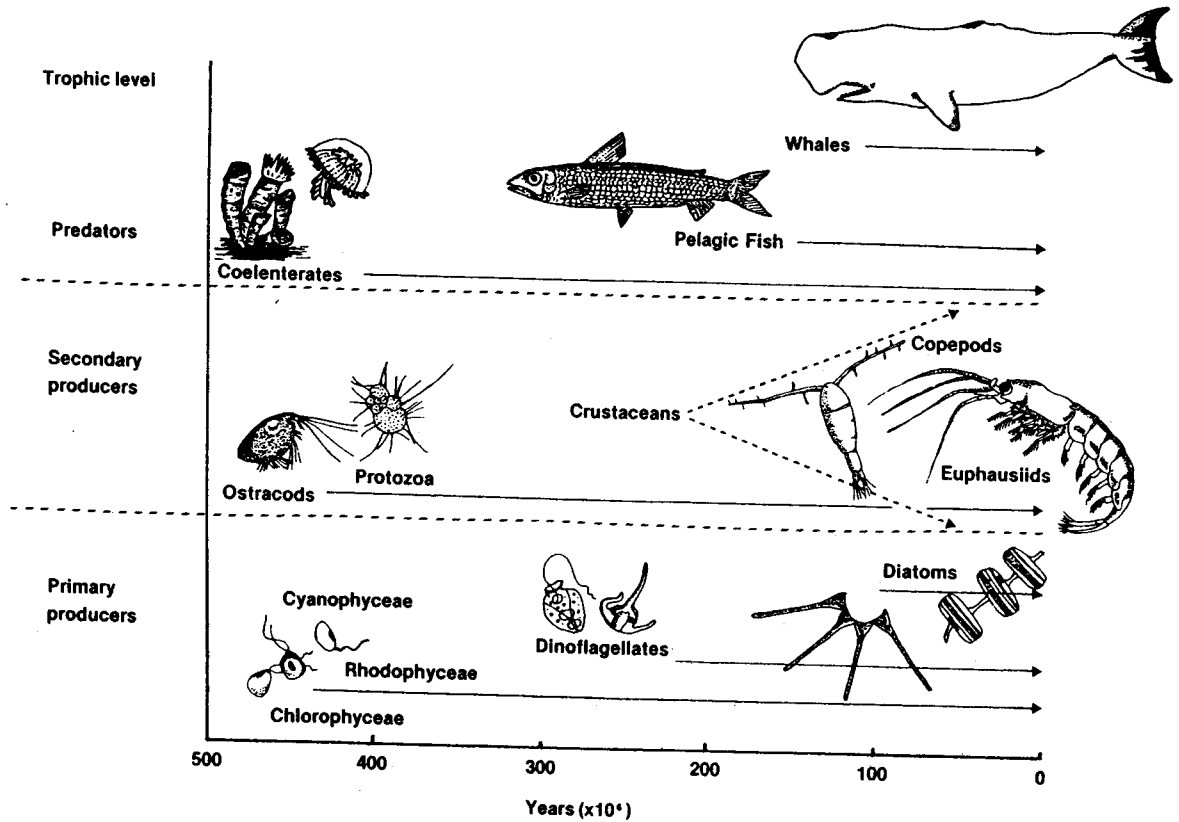


Fig. 4. The evolution of three food chains in the pelagic environment of the sea from the Cambrian to the present (for explanation see text and references).

the appearance of diatoms<sup>21,22</sup> which eventually allowed for the evolution of a third food chain in which the top predators were homiothermic whales, having a metabolic energy requirement some 30 times greater than that of heterothermic fish and vastly in excess of that of more primitive organisms.<sup>19</sup> This latter event has been advanced by Lipps and Mitchell<sup>26</sup> to account for radiations and declines in pelagic marine mammals; the emphasis in this latter hypothesis is that since whales are even more metabolically costly than fish, their evolution and maintenance had to be accompanied by a large increase in the efficiency of pelagic production at the primary level. Thus whales were shown by Cushing<sup>27</sup> to feed in areas especially rich in plankton, that is, upwelling regions.

The diatoms, through their tendency to form chains, present the largest spectrum of prey size to the secondary producers. In addition, they contain an accessory pigment system (chlorophyll *c* and fucoxanthin) which is similar to that of the dinoflagellates and are therefore capable of efficient photosynthesis at depth.<sup>24</sup> However, their advantage over flagellates, including dinoflagellates, appears to be in their high growth potential, which has been discussed above. The disadvantage of diatom growth lies in the lack of flagella; consequently, they are less competitive with flagellates in stable water masses, that is, outside of upwelling areas and regions of coastal turbulence. With the arrival of diatoms the ocean's productivity in certain areas was greatly increased; the elaboration of the secondary producers into the present-day crustacean communities, which probably started in the early Devonian, continued in the late Cretaceous and early Cenozoic with the establishment of such important pelagic herbivores as the euphausiids.<sup>25</sup>

The importance of the evolution of certain classes of phytoplankton in determining the trophic structure of the sea is summarized in Table 1, from which it can be seen that the changes in the properties of the phytoplankton from left to right result in a higher form of energy being available to the next trophic level, and subsequently the support of more advanced forms of life in the sea, from jellyfish to fish and finally mammals.

### Summary and conclusions

An attempt has been made to show that the upwelling ecosystem is an integral part of the ecology of the pelagic ocean, that it can be defined experimentally in large part in terms of the physiological properties of its phytoplankton and that, in an evolutionary sense, it represents the youngest biological ecosystem in the pelagic environment. It is sustained by exometabolic energy and because of its large energy requirements it is possibly a most fragile ecosystem. From experiments as well as natural observations, Greve and Parsons<sup>17</sup> have discussed how the effects of man's fishing and pollution

Table 1. Properties of algal classes which could change the amount of energy made available to the next trophic level, as discussed in the text.

Property and Result	Algal Class		
	Rhodophyceae Myxophyceae Chlorophyceae	Dinophyceae (Dinoflagellates)	Bacillariophyceae (Diatoms)
Size	small	large	largest
Resultant; (i) prey more easily captured by raptorial feeders (ii) shorter food chains			→
Pigments	no 'blue' pigments	chlorophyll <i>c</i> + peridinin	chlorophyll <i>c</i> + fucoxanthin
Resultant; Greater utilization of light with depth			→
Cell Division	slow	slow	rapid
Resultant; More food delivered to the ecosystem per unit time			→

might effect changes in the natural ecology of the ocean. In the former case it was demonstrated that diatoms are more susceptible to certain pollutants, such as heavy metals, than flagellates. It has yet to be determined if the removal of raptorial feeders by the world's fisheries will affect the balance of top predators and favour the establishment of increased numbers of jellyfish. However, climatic change could greatly influence the diatom/flagellate ratio and thereby alter the trophic nature of the sea.

In these discussions I have omitted much detail in order to achieve a relatively simple presentation in which energy-rich and energy-poor ecosystems are seen to have evolved quite differently. In particular, I have not considered other top predators, such as birds, reptiles and cephalopods. Further, the impression may have been gained that the upwelling ecosystem is dominated by large raptorial feeders, while in fact it is largely a filter-feeding system — consider the role of the anchovy and baleen whales. However, the pathways described appear reasonable if we consider that ecological modifications will also have occurred with time. Thus, in the case of baleen whales it is tempting to comment that these creatures essentially evolved a better filter system than the jellyfish by bringing the filtering apparatus inboard where it became structurally stronger and more efficient. The strategy of filtering food from the sea has therefore gone full cycle from the most primitive to the most complex organisms, the latter requiring much more energy than the former.

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