BULLETIN OF MARINE SCIENCE, 71(1): 13–16, 2002

CEPHALOPOD BIOMASS AND PRODUCTION: AN INTRODUCTION TO THE SYMPOSIUM

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Worldwide interest has been generated in the apparently large biomass of cephalopods in the global oceans, its importance in marine food webs, especially at higher trophic levels, and to major international and regional fisheries (Clarke, 1996). Commercial fisheries globally take up to 3 million tonnes of cephalopods annually. This quantity has risen steadily over the last three decades, and the cephalopod resource category is one of few in which catches have increased during this period. At the same time, improved methods of species identification and size estimation of the cephalopods taken in the diet of many marine predators have suggested total removals by predators to be at least 100 fold greater than human fisheries.

Rapid advances have been made in understanding key life cycle processes of cephalopod development, feeding, growth, reproduction, and mortality; the factors underpinning cephalopod productivity; and the interactions between these biotic factors and the physical environment. They have shown that cephalopods reach large individual body sizes and are extremely fast-growing. Key aspects of their ability to achieve these high growth rates are their exclusively predatory feeding habits and high growth efficiency (food conversion). Unlike fish and other invertebrates they do not seem to attain an asymptotic adult size before reaching reproductive maturity. The coastal cephalopods breed over a short period of time and death follows shortly afterwards. They are essentially annual species in which there is little overlap of successive generations. In these circumstances, the biomass from any one species is likely to be available to predators and fisheries for only a limited period of time (Boyle, 1990).

Presently there is no overall conceptual framework to match these very high estimates for standing crop biomass (from predators and fisheries) with the life cycle characteristics of the coastal species and the productive capacity of the environment. Examination of the available factual information on this subject raises a series of focal questions which might help to shape the future scientific agenda for cephalopod ecologists.

The global biomass (standing stock of adults and sub-adults) of cephalopods in the oceans has been variously estimated from 193 to 375 million tonnes (Rodhouse and Nigmatullin, 1996). These figures have been derived by tentatively accumulating the estimate ranges for mesopelagic squid ($150–300 \times 10^6$ t); oceanic epipelagic squid ($30–50 \times 10^6$ t); slope/shelf-edge squid ($8–15 \times 10^6$ t); and shelf sepioids and octopuses ($5–10 \times 10^6$ t). Cephalopods of all types are consumed by a variety of top predators; large fishes (Smale, 1996), marine mammals (Clarke, 1996; Klages, 1996; Santos et al., 2001) and birds (Croxall and Prince, 1996). No cumulative estimate of consumption by these large predators is available, but sperm whales alone could account for an annual biomass of $213–320 \times 10^6$ t of cephalopods from open ocean areas (Clarke, 1996).

The primary question as to whether these apparently massive estimates of biomass are realistic; whether they are compatible with other global estimates of marine productivity and consistent with the productive potential of cephalopods; has yet to be addressed.

Can Squid Really Feed Marine Top Predators?

Using fisheries data alone and considering only flows of matter (catches and food consumption) between trophic levels, the primary production required to sustain total global fisheries, including the discarded by-catch, has been estimated to be about 8% of total aquatic primary productivity (Pauly and Christensen 1995). The cephalopod component of this estimate was 2.476×10^6 t (mean annual wet weight for 1988–1991), accounting for 1.88% of their estimate for the primary production removed by fisheries. Human fisheries for cephalopods have since continued to rise, reaching $>3.0 \times 10^6$ t in 1996. Extrapolation of this approach (Pauly and Christensen, 1995) to include 267×10^6 t for 'removal' of adult/sub-adult cephalopods consumed by major predators (the mean annual consumption estimate for sperm whales alone), would require primary production of 2 × the estimate for total global fisheries, or as much as 16% of the total for the aquatic ecosystem! This fraction may not be as unlikely as it first seems if marine mammals are harvesting deep sea squids and fishes generally not available to human fisheries (Trites et al., 1997). *Does consumption by predators mean biomass removal?*

Factors which could contribute to an over-estimation of cephalopod biomass include the possible exaggeration of their incidence in predator diets because cephalopod remains persist longer than those of other prey. Without estimates of residence time, and in the absence of good information on degradable soft tissues of prey, an over-emphasis on cephalopods in the diets is probable. It may be significant that the apparent incidence of cephalopods in the diet of stranded whales greatly exceeds that recorded in comparable animals killed by whaling (Santos et al., 1999). *Can the potential estimation errors be controlled?*

The scaling up of limited predator and fishery data to ocean basin scales and the low carbon content (watery tissues) of many meso-pelagic cephalopods, also introduces a great degree of uncertainty since this (the meso-pelagic fauna) is the largest component of the accumulated biomass estimate. *What are the uncertainties of scaling up by quantity and area?*

Life cycle characteristics are key influences on the rate of delivery of biomass to predators. The cephalopod life cycle paradigm is remarkably consistent across the neritic and coastal groups of octopods, sepioids (cuttlefish), loliginid squid, and those epipelagic ommastrephid squid which venture on to the shelf for feeding excursions (Boyle, 1983, 1987). These exclusively carnivorous species have high growth rates, uniseasonal reproduction and a short, endogenously determined lifespan; characteristics consistent with high biomass turnover rates or annual production/biomass ratios. For these cephalopods there is annual build and crash of biomass with little overlap of generations; the annual population results from the relative success of recruitment and the post-spawning adult biomass is available for predation without directly affecting the next generation. This pattern is most extreme when there is a short breeding season during which the whole population breeds more or less synchronously, but is mitigated in cases where there is extended duration of the breeding season, batch spawning, or trends towards the asynchronous spawning of cohorts within the population (Boyle and Boletzky, 1996). These populations are subject to high variability due to environmental factors and may be considered to have a low 'inertia' leading to wide and currently unpredictable fluctuations both in location and density. *What influences the rate of delivery of cephalopod biomass to predators?*

Large size and generous yolk provision for embryos (in the coastal species spawning benthic egg masses) and their early attainment of adult size and breeding status, must reduce mortality rates in young stages. Taken together with the high incidence of cannibalism reported in many cephalopods (especially migratory species) these life cycle characteristics will contribute to the sequestration of a high proportion of total production by a species into the adult population. *Does short lifespan in coastal species contribute low mortality rates in young stages?*

Estimates for the individual trophic efficiency of cephalopods are unusually high, with estimates for gross conversion efficiency (weight of food consumed/somatic weight gain) ranging between 13% for active squid species to 69% for the more sedentary octopuses during periods of peak growth (Wells and Clarke, 1996). This may mean that the commonly used figure of 10% for energy transfer between ecological trophic levels (Pauly and Christensen, 1995) is unduly conservative. *Is the commonly used figure of 10% energy transfer between ecological trophic levels unduly conservative for coastal cephalopods?*

Life cycle characteristics of the coastal cephalopods, therefore, suggest that biomass production can occur at high rates, and that a particularly high proportion of it may be available for consumption by predators or capture by fisheries. *Is an especially high proportion of total production by a cephalopod species sequestered in the adult population?*

The major part of the global cephalopod biomass estimate, results from inflation by area across that 85% of the marine province which is oceanic and where cephalopods may be distributed in quantity to depths of at least 600 m. Biological knowledge of the majority of oceanic pelagic forms is lacking although most systematic diversity in cephalopods is present in the meso- and bathy-pelagic environments. Some studies suggest the cephalopod biomass in the open sea (nektonic) to be about half that of fish (Maynard et al., 1975) but the mismatch between direct sampling with nets and indirect sampling from higher predators in this environment is well known (Clarke, 1977). Although lower cephalopod metabolic rates at depth suggest lower productivity (Seibel et al., 1997), available evidence does not allow general biological conclusions. A greater range of life cycle features is probable. The slope octopus *Opisthoteuthis* (600–1400 m), for example, appears to breed continuously over the majority of its growth period (Villanueva, 1992); in contrast, the meso-pelagic (200–600 m) enoploteuthid squid *Watasenia scintillans*, moves into shallow water during annual spawning aggregations which are followed by population-scale post-spawning mortality at an estimated age of only 11–13 mo (Hayashi, 1993). *In what respects do oceanic and mesopelagic cephalopod forms resemble the coastal species?*

The life cycle characteristics and ecology of the oceanic and mesopelagic cephalopod fauna, in particular, need to be established before current estimates for global cephalopod biomass can be reconciled with their biological productive capacity and that of the marine ecosystem in total. We must begin to understand whether the life cycle features established for the coastal species represent special cases, or the degree to which they may be generalized to the much greater oceanic and deepwater fauna.

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