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and the other π face shielded by the catalyst, and are all expected to be energetically accessible under the reaction conditions. Computational analyses using either density functional theory or ab initio methods (Fig. 4, C to E) predict that the enantioselectivity-determining cycloaddition occurs preferentially with complex **I**, leading to the experimentally observed (*R*)-enantiomer of product **4a_{exo}**. The lowest-energy cycloaddition transition structure displays iminium N–H \cdots O_{sulfonamide} and formyl C–H \cdots O_{sulfonate} hydrogen bonds (Fig. 4C), and is predicted to have ≥ 1.3 -kcal/mol lower energy than alternatives arising from complexes **II** to **IV**, which is consistent with the experimental data. The basis for enantioselectivity may be ascribed to a stabilizing π – π interaction between the (CF₃)₂–C₆H₃N component of the catalyst and the cationic aniline moiety of the substrate. This interaction is evident in transition structures leading to the major enantiomer of **4a_{exo}** (Fig. 4D), but it is absent in transition structures leading to the minor enantiomer (Fig. 4E).

Enantioselective catalysis by **1a** of a strong Brønsted acid-catalyzed Povarov reaction thus involves tight binding to a highly reactive cationic intermediate through multiple, specific H-bonding interactions, and these noncovalent interactions are maintained in the subsequent stereo-determining cycloaddition event. One of the four energetically accessible ground-state complexes undergoes reaction with the nucleophile preferentially, illustrating the ability of bifunctional catalyst **1a** to control precisely the outcome of this reaction through noncovalent interactions

alone. Given the known ability of urea and thiourea derivatives to bind a wide range of anions, the strategy demonstrated here is applicable, in principle, to cationic intermediates with a variety of counterion structures.

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Materials and Methods

SOM Text

Figs. S1 to S19

Tables S1 to S17

References

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100-Million-Year Dynasty of Giant Planktivorous Bony Fishes in the Mesozoic Seas

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Large-bodied suspension feeders (planktivores), which include the most massive animals to have ever lived, are conspicuously absent from Mesozoic marine environments. The only clear representatives of this trophic guild in the Mesozoic have been an enigmatic and apparently short-lived Jurassic group of extinct pachycormid fishes. Here, we report several new examples of these giant bony fishes from Asia, Europe, and North America. These fossils provide the first detailed anatomical information on this poorly understood clade and extend its range from the lower Middle Jurassic to the end of the Cretaceous, showing that this group persisted for more than 100 million years. Modern large-bodied, planktivorous vertebrates diversified after the extinction of pachycormids at the Cretaceous–Paleogene boundary, which is consistent with an opportunistic refilling of vacated ecospace.

The largest vertebrates—fossil or living—are marine suspension feeders. Modern clades adopting this ecological strategy diversified in the Paleogene (66 to 23 million years ago) (1–3) and include baleen whales and four independent lineages of cartilaginous fishes (sharks and rays) (4). In striking contrast to the

array of giant suspension feeders found in Cenozoic marine environments, this guild has appeared to be absent during most of the Mesozoic, an interval that is marked by the ecological ascendancy of modern plankton groups (5, 6). Possible candidates have been proposed (7, 8), but the clearest examples of large-bodied planktivores in

the Mesozoic seas have been a handful of bony fishes confined to a brief 20-million-year window during the Jurassic (Callovia-Tithonian, 165 to 145 million years ago) and known almost exclusively from European deposits (9–12). These enigmatic taxa belong to the extinct family †Pachycormidae (the dagger symbol indicates extinct groups), a stem-teleost clade that is otherwise composed of pelagic predators convergent upon tunas and billfishes (10). Giant †pachycormids include the largest bony fish of all time (the ~9 m †Leedsichthys) (9, 13), but their short stratigraphic range had implied that they were an inconsequential component of

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Mesozoic marine ecosystems and a minor—and ultimately unsuccessful—experiment in suspension feeding at large body sizes.

Here, we report newly recognized remains of suspension-feeding †pachycormids ranging from the lower Middle Jurassic to the Upper Cretaceous and discuss the implications of our discoveries for Mesozoic marine ecosystems. With the exception of one recently discovered specimen, these fossils were housed in museum collections in which they were either unstudied or had been described but incorrectly identified in the 19th century. Further preparation and examination, combined with an existing systematic framework (10, 12), led us to revise previous interpretations of this material.

The fossils reported here include a generically indeterminate cranium from the lower Middle Jurassic (Bajocian, 172 to 168 million years ago) Inferior Oolite of Dorset, UK (Fig. 1); the nearly complete skull of †*Rhinconichthys taylori* gen. et sp. nov. (14) from the lower Upper Cretaceous (Cenomanian, 100 to 94 million years ago) Lower Chalk of Kent, UK (Fig. 1); a similar fish from the Upper Cretaceous (Cenomanian) Middle Yezo Group of Hokkaido, Japan (15); and multiple specimens of †*Bonnerichthys gladius* gen. nov. (16) from mid-upper Upper Cretaceous (Coniacian-Maastrichtian, 89 to 66 million years ago) deposits of the Western Interior Seaway and Coastal Plain in the United States (Fig. 2) (15, 17, 18).

These specimens reveal the anatomy of suspension-feeding †pachycormids, previously known exclusively from poorly understood Jurassic fossils. Material of †*Leedsichthys* is crushed, fragmented, and disarticulated (9, 11), and detailed structure is obscure in rare articulated examples of †*Asthenocormus* (10) and †*Martillichthys* (12). We base our description on †*Bonnerichthys* (Fig. 2).

The snout is covered by a median rostrodermethmoid, which is a †pachycormid synapomorphy (10, 15, 19). Two lateral projections along the oral margin are unknown in other forms, but their position suggests that they might be co-ossified premaxillae. Thickened ridges trace the lateral margins of the rostrodermethmoid, mark the position of the supraorbital canal, and imply that the rostrodermethmoid of †*Bonnerichthys* also incorporates the nasals. The rectangular frontal bears a ridge on its visceral surface, marking the course of the supraorbital sensory canal. The hook-shaped dermosphenotic lies lateral to the frontal, defines the dorsal margin of the orbit, and bears the anastomosis between the infraorbital and otic sensory canals. A triradiate canal-bearing ossification is identified as a dermopterotic. There is no indication of sutural contacts between the dermosphenotic, dermopterotic, and frontal, or between the frontal and the rostrodermethmoid. The condition in †*Bonnerichthys* is derived relative to all other †pachycormids, in which dermal bones of the skull roof are tightly linked.

As in many suspension-feeding fishes (4), the dentary of the lower jaw and the maxilla of

the upper jaw are elongate and edentulous. Absence of dentition even extends to the prearticular, which lines the inner surface of the mandible, and the parasphenoid, which forms much of the roof of the oral chamber. The parasphenoid is pierced by paired foramina for the internal carotid arteries, a derived feature of teleosts (15).

Members of the operculular series recovered for †*Bonnerichthys* include the opercle, subopercle, and gular plate. The hyoid arch is represented by large, imperforate hyomandibulae with well-developed opercular processes and rod-shaped ceratohyals. Gill-arch remains include hypo- and infrapharyngobranchials with complex articular surfaces, plus long and deeply grooved cerato- and epibranchials. Enlarged gill rakers bearing long, needle-like projections are found in †*Asthenocormus*, †*Leedsichthys*, and †*Rhinconichthys* (9, 10, 12, 15). These probable suspension-feeding structures have not yet been recovered for †*Bonnerichthys*.

Typical of †pachycormids, the pectoral fins are scythe-shaped. The leading edge of the fin is fused, with an irregular margin that contrasts with the precisely patterned serrations in some

species of †*Protosphyraena* (10, 17, 19, 20). Distally, the fin-rays bifurcate in the “Y” pattern characteristic of †pachycormids (10, 19). The pectoral endoskeleton of †*Bonnerichthys* agrees closely with those of †*Orthocormus* (21) and †*Protosphyraena* (20). The second radial is “C”-shaped, makes two independent articulations with the primary shoulder girdle, and is trailed by a series of paddle-shaped radials (15).

The skull of †*Bonnerichthys* specimen KUVV 60692 measures roughly 1 m from the tip of the snout to the rear of the pectoral girdle (Fig. 2C). Isometric scaling relative to articulated fossils of †*Asthenocormus* and †*Martillichthys* (12) suggests a total length of approximately 4 m for this specimen. Other less complete remains of †*Bonnerichthys* (associated skeleton University of Nebraska State Museum UNSM 88507 and pectoral fins and girdles KUVV 465) are over 20% larger than equivalent elements of KUVV 60692, indicating that the genus is likely to have reached at least 5 m in length. This is smaller than revised length estimates for †*Leedsichthys* (13) but approaches the size of some modern planktivorous chondrichthyans (4, 22).

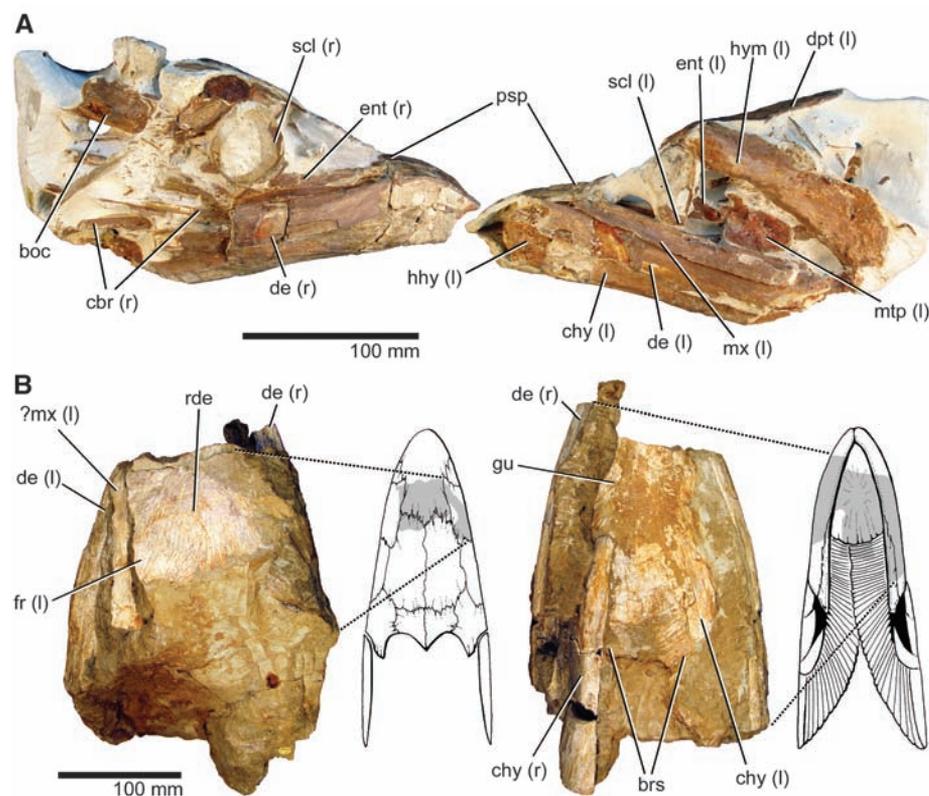


Fig. 1. Newly recognized fossils of giant Mesozoic suspension-feeding bony fishes. **(A)** †*Rhinconichthys taylori* gen. et sp. nov., BMNH 219, from the lower Upper Cretaceous (Cenomanian) Lower Chalk of Kent, UK, in right- and left-lateral views. **(B)** Indeterminate edentulous †pachycormid, BMNH P.41669, from the lower Middle Jurassic (Bajocian) Inferior Oolite of Dorset, UK, in dorsal and ventral view (anterior is toward the top). Matrix has been digitally masked so as to enhance contrast, and preserved bone that would have been visible externally in the ventral and dorsal views is shaded in tentative reconstruction based on †*Martillichthys* and †*Pachycormus*. Scale bars apply only to fossils. boc, basioccipital; brs, branchiostegal rays; cbr, ceratobranchials; chy, anterior ceratohyal; de, dentary; dpt, dermopterotic; ent, entopterygoid; fr, frontal; gu, median gular; hhy, hypohyal; hym, hyomandibula; mtp, metapterygoid; mx, maxilla; psp, parasphenoid; rde, rostrodermethmoid; and scl, sclerotic ring. Paired bones are listed as right (r) or left (l).

Fig. 2. †*Bonnerichthys gladius* gen. nov., a giant suspension-feeding bony fish from the Upper Cretaceous of the United States. (A) Neurocranium and parasphenoid in ventral view. (B) Gular plate in ventral view. (C) Cranial and pectoral skeleton, shown in right-lateral view. Bones that were reconstructed from other specimens are shown in gray. (D) Hypural plate in right-lateral view. Scale bar in (C) applies to (A) to (D). (A) to (C) show specimen KUPV 60692; (D) shows specimen FHSM (Sternberg Museum, Hays, Kansas) VP-17428. (E) Tentative reconstruction in ventral (top) and lateral (bottom) views, indicating life position of bones shown in (A) to (D). ant, antorbital; ar, articular; cle, cleithrum; dsp, dermosphenotic; ect, ectopterygoid; f.hym, hyomandibular facet of neurocranium; op, opercle; p.f, pectoral fin; qu, quadrate; sco, scapulocoracoid; and sop, subopercle. Other abbreviations are as in Fig. 1.

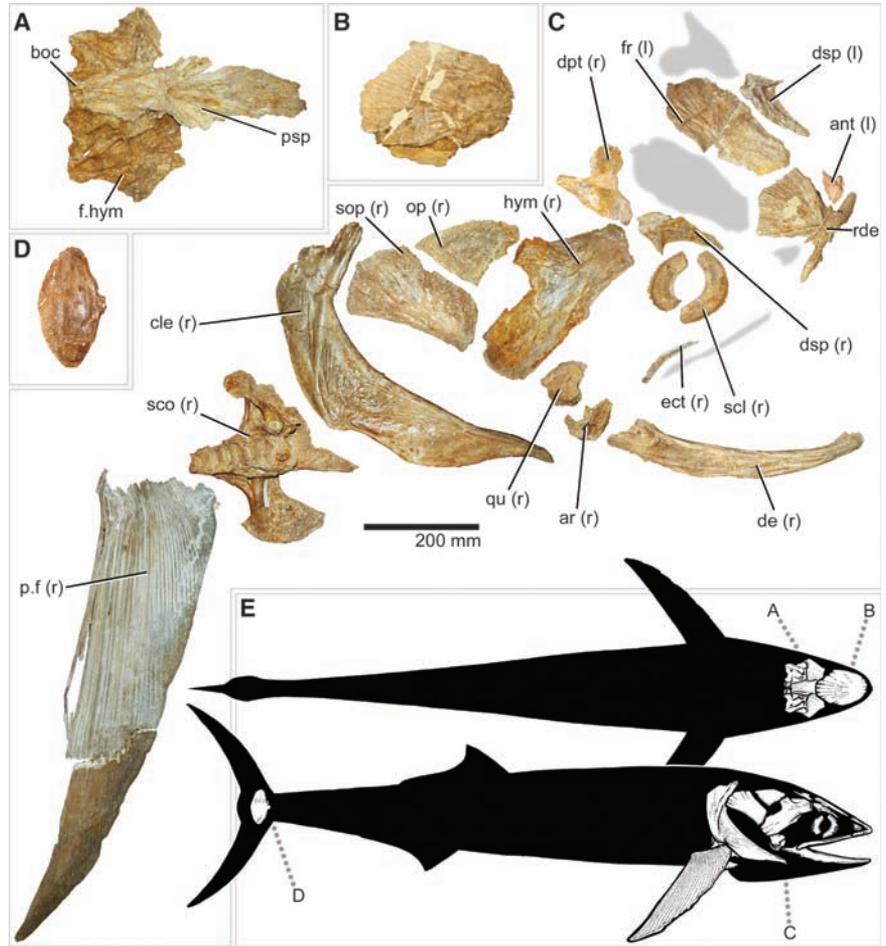
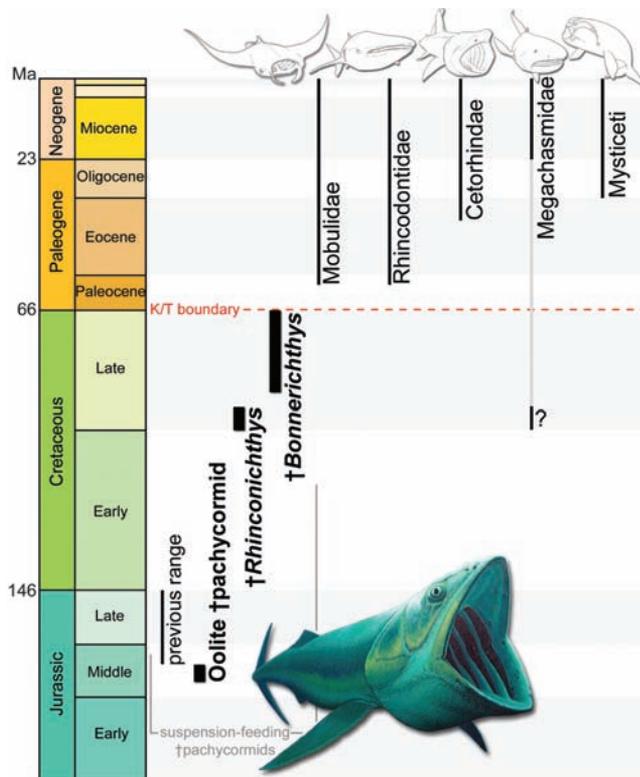


Fig. 3. Stratigraphic distribution of giant †pachycormid fishes and modern planktivorous whales and chondrichthyans (icons of living groups are not shown to scale). Previous occurrences of suspension-feeding †pachycormids were confined to a short interval in the Jurassic (shown as a thin line representing †*Leedsichthys*, †*Martillichthys*, and †*Asthenocormus*), but occurrences reported here (shown as thick lines) expand this group's stratigraphic range to approximately 100 million years. Convincing records of modern large-bodied planktivorous vertebrates only appear in the Paleogene, after the extinction of giant †pachycormids.



A cladistic analysis provides robust support for the monophyly of a clade comprising †*Bonnerichthys* plus other large edentulous †pachycormids and reinforces the interpretation of †pachycormids as stem teleosts (15). This subset of †pachycormids is a unique example of suspension feeding at massive body sizes within the teleost total group (23), which is a diverse radiation that otherwise contains a bewildering array of bodyplans and whose living representatives are taxonomic dominants in marine vertebrate faunas (22). With lengths between 5 and 9 m, †*Bonnerichthys* and †*Leedsichthys* are comparable in size with some modern suspension-feeding sharks (4, 22). Even the more modestly sized †*Martillichthys* and †*Asthenocormus* are ecological giants in comparison with extant planktivorous teleosts. At over 2 m, these †pachycormid genera are an order of magnitude longer—and by extension several orders of magnitude more massive—than living teleost suspension feeders, most of which are on the order of 10 cm long (23). The only moderately large planktivorous actinopterygian (the more extensive bony fish clade that contains teleosts) is the paddlefish *Polyodon*. This sturgeon relative is confined to the freshwaters of North America and rarely exceeds 2 m in length despite a greatly elongated rostrum (24).

The discovery of early Middle Jurassic and Late Cretaceous †pachycormids with anatomical features that are consistent with suspension feeding (4) alters the picture of the evolution of this ecological guild in the Mesozoic and afterward. Oceans during much of this interval have been viewed as devoid of large-bodied suspension feeders (25), but we now recognize that †pachycormids occupied this ecological role for much of the Mesozoic (Fig. 3). Marine reptiles diversified prolifically during this geological interval, attaining massive sizes and evolving specializations attributed to suction and ram feeding (26), but there is no clear evidence that they ever adopted planktivory. This observation, coupled with the perceived absence of large-bodied planktivores during most of the Mesozoic, led to suggestions that anatomical constraints prevented these otherwise diverse marine amniote clades from exploiting suspension feeding (25). Our findings suggest that marine reptiles might have been excluded from this trophic strategy by incumbent †pachycormids.

The first fossil occurrences of modern large-bodied suspension feeders are confined to the Cenozoic: manta rays and whale sharks in the late Paleocene (1), basking sharks in the mid-Eocene (2), and plankton-feeding whales near the Eocene-Oligocene boundary (3). The only example with a possible Mesozoic record is the megamouth shark *Megachasma*, but there is a 75-million-year interval between a few isolated Late Cretaceous teeth and the next oldest occurrence, which dates to the late Oligocene–early Miocene (27). The radiation of large-bodied suspension-feeding chondrichthyans and whales in the Paleogene follows the disappearance of †*Bonnerichthys* and many other large-bodied marine teleosts (28, 29) during the end-Cretaceous extinction, suggesting that familiar modern groups of planktivores diversified into the ecospace vacated by giant †pachycormids.

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- Etymology: The generic name is a homophone of an unpublished name by G. Mantell (“*Rhynchonichthys*”) and evokes the whale shark *Rhincodon*. The specific name honors H. W. Taylor, collector of the type. Systematics: Osteichthyes Huxley, 1880; Actinopterygii Woodward, 1891; Teleostei Müller, 1846 (*sensu de Pinna* 1996); †Pachycormidae Woodward, 1895; and †*Rhynchonichthys taylori* gen. et sp. nov. Holotype: BMNH (The Natural History Museum, London) 219, nearly complete three-dimensional skull lacking anterior skull roof and posterior portions of lower jaws. Diagnosis of genus and species: Edentulous †pachycormid differing from other members of that group in having exceptionally elongated posterior processes of the dermopterotics and a proximal head of hyomandibula rounded rather than laterally compressed. Locality and age: Lower Chalk (Late Cretaceous, Cenomanian), Burham, Kent, UK.
- Materials and methods are available as supporting material on *Science* Online.
- Etymology: The generic name honors the Bonner family, Scott City, Kansas, which has made many important discoveries in the Niobrara Formation, including KUVF (University of Kansas Natural History Museum, Lawrence, Kansas) 60692. Systematics: Osteichthyes Huxley, 1880; Actinopterygii Woodward, 1891; Teleostei Müller, 1846 (*sensu de Pinna* 1996); †Pachycormidae Woodward, 1895; †*Bonnerichthys* nov. gen.; and †*Bonnerichthys gladius* (Cope, 1874), comb. nov. Holotype: AMNH (American Museum of Natural History, New York) FF 1849, incomplete pectoral fin. Diagnosis of genus and species: Edentulous †pachycormid differing from other members of that group in having a rostrodermethmoid with ventrolateral processes, basioccipital with deep aortic groove, dermal bones of skull unsutured, and anterior margins of pectoral fins irregularly crenellated. Locality and age: Type from Niobrara Formation (Late Cretaceous, Coniacian–Campanian), Kansas, USA.
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SOM Text
Figs. S1 to S15
References

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Climate, Critters, and Cetaceans: Cenozoic Drivers of the Evolution of Modern Whales

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Modern cetaceans, a poster child of evolution, play an important role in the ocean ecosystem as apex predators and nutrient distributors, as well as evolutionary “stepping stones” for the deep sea biota. Recent discussions on the impact of climate change and marine exploitation on current cetacean populations may benefit from insights into what factors have influenced cetacean diversity in the past. Previous studies suggested that the rise of diatoms as dominant marine primary producers and global temperature change were key factors in the evolution of modern whales. Based on a comprehensive diversity data set, we show that much of observed cetacean paleodiversity can indeed be explained by diatom diversity in conjunction with variations in climate as indicated by oxygen stable isotope records ($\delta^{18}\text{O}$).

Modern cetaceans (Neoceti), the mysticetes and odontocetes, show a number of mass-feeding adaptations beyond the immediate demands of an aquatic existence (1). Whereas mysticetes have become edentulous and rely on baleen to filter food from the water, odontocetes have evolved the ability to search for prey by means of echolocation. What unites these two different adaptive strategies is their effectiveness in terms of mass feeding:

Whereas mysticetes obtain enormous amounts of small prey by filtering vast quantities of water, odontocetes may be able to use their biosonar to locate the vertically migrating layers of plankton with their associated grazers and predators known as deep scattering layers (1). To support such large and abundant apex predators, the ecosystems exploited by cetaceans must be extremely productive, and the energy captured by primary producers must be transmitted very efficiently