Coexistence of fish species with strongly similar life histories – population dynamical feedback forces species to pick sides

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Summary

Fish generally grow several orders of magnitude between the larval and adult stage. Many ecological properties of organisms are related to body size, and hence small fish often have very different ecological roles than large conspecifics. This also implies that omnivory, the feeding on more than one trophic level by individuals of the same species, is a common phenomenon in fish. Intraguild predation is omnivory in its simplest form, where two species compete for the same resource, but one of the species can also eat its competitor. In models, persistence of both species in such a configuration is difficult to obtain. In marine fish communities however, it is observed routinely. One way in which persistence of omnivorous species can be established is by incorporating it as an ontogenetic diet shift, where small individuals of both species compete, and large individuals of one can feed on the small individuals of the others species. We show in this study that this mechanism can not only lead to persistence of a single omnivorous species, but also to persistence of multiple omnivorous species. This is possible given that the adults have sufficiently different diets. It is shown that, while adults of both species can feed both on small competitors or on the basic resource, due to the population dynamical feedback, one species will in practice act as a predator, while the other acts as prey. This way, a system with two omnivores in practice persists as a tritrophic system. Which of the species assumes which role depends on the specific community characteristics. We show here that by incorporating complex size-dependent feeding relationships in food webs, many more species may be able to coexist than is possible based on either species-level considerations or size spectrum models which do incorporate within-population size differences, but relate diet only to individual body size irrespective of species identity. The mechanism underlying our result may be part of the explanation why fish species with seemingly similar life histories do coexist in marine ecosystems.

1 Introduction

Omnivory is defined as the feeding on different trophic levels (Pimm and Lawton 1978), which allows a species (an intraguild predator) to simultaneously prey on and compete with another species (its intraguild prey). The basic form of this type of interaction is also referred to as intraguild predation (IGP: Polis et al. 1989, Holt and Polis 1997). IGP has received considerable attention since it is shown to be common in natural communities (Polis 1991, Polis and Strong 1996, Arim and Marquet 2004). Theoretical predictions, however, show limited scope for coexistence of intraguild predators and intraguild prey (Holt and Polis 1997, Diehl and Feissel 2000, Mylius et al. 2001). Holt and Polis (1997) formulated two necessary conditions for coexistence in IGP systems, namely that the intraguild prey (or intermediate consumer) should be superior in resource competition and that productivity levels should be intermediate. In systems with low productivity resource competition plays the most dominant role, since consumer density is too low to be beneficial for the intraguild predator, eventually leading to predator extinction. In contrast, in highly productive systems intraguild predators become too abundant and hence predation too intense for the consumer to persist. Coexistence is therefore maintained only at intermediate productivity levels when competition and predation are by and large balanced. Many subsequent studies have focused on possible mechanisms that promote coexistence of intraguild prey and predators, given that IGP and omnivory are common in natural systems. Among the mechanisms originally proposed by Holt and Polis (1997) are age-restricted predation or prey life stages invulnerable to predation (Mylius et al. 2001, Borer 2002, Rudolf and Armstrong 2008), adaptive foraging behaviour by intraguild predators (Krivan 2000, Krivan and Diehl 2005), spatial or temporal refugees for the intraguild prey (Finke and Denno 2006, Janssen et al. 2007, Amarasekare 2008, Okuyama 2008) or additional resources for intraguild prey (Holt and Huxel 2007) or intraguild predator (van de Wolfshaar et al. 2006). In theory, these mechanisms may enhance coexistence of consumers and predators by extending the conditions under which competition and predation are balanced. This effect is, however, often rather marginal, as exemplified by the study by (Borer 2006), which showed that adding biological detail is not likely to increase coexistence possibilities in an empirically parameterized IGP model. More commonly, these mechanisms increase coexistence by reducing the strength of the competitive interactions between intraguild predators and prey to a negligible level, which effectively marginalizes the IGP nature of the interaction (simultaneous predation and competition). In this sense the frequent occurrence of IGP can still only be understood when it's a relatively weak interaction (Janssen et al. 2006).

Omnivory often results from changes in body size over ontogeny (Polis et al. 1989). As many species grow considerably in size during their life, ecological traits that scale with body size such as metabolic rate, risk to predation, resource availability and exploitation rate change over ontogeny (Peters 1983, Werner and Gilliam 1984). Species may therefore shift habitat or feed on different resources in different life stages, a phenomenon referred to as ontogenetic niche shift (Werner and Hall 1979, Werner and Gilliam 1984, Mittelbach 1988, Olson et al. 1995), or life-history omnivory (Pimm and Rice 1987). A species could therefore be an omnivore when considering its entire life, but a specialist when considering separate life stages. When intraguild predation involves life history, adult intraguild predators prey on consumers, while juvenile intraguild predators compete with consumers for a shared resource. Feeding on different prey types during different life stages is generally associated with a trade-off in feeding efficiency, so that predators are inferior in resource competition to their specialist prey species (Werner and Gilliam 1984, Persson 1988). Competing for a shared resource at an early life stage may therefore limit recruitment of juvenile predators to later life stages and thus result in a juvenile competitive bottleneck (Werner and Gilliam 1984, Neill 1988, Persson and Greenberg 1990, Byström et al. 1998). Walters and Kitchell (2001) dubbed this the cultivation effect, since dominant large species in this way cultivate a favourable environment for their young. When species that are dependent upon cultivation for their persistence, collapse and reach low abundances, a juvenile competitive bottleneck can prevent recovery although the species would be able to persist once present owing to the cultivation by adult predators.

Although life-history omnivory and ontogenetic niche shifts are a widespread phenomenon (Werner and Gilliam 1984, Polis et al. 1989), their impact on the dynamics of IGP is only studied to a limited extent (Mylius et al. 2001, van de Wolfshaar et al. 2006, Hin et al. 2011). Nevertheless, Hin et al. (2011) showed that intraguild predation with a life-history omnivore permits coexistence of predator and prey over more than just intermediate resource productivities and no longer requires the prey to be the better competitor for resource. This occurs because Hin et al. (2011) assume that the adult intraguild predator requires intraguild prey for survival, which means that the predator by definition can never exist in the system in absence of the intraguild prey and hence also cannot outcompete it. Other studies that explicitly focus on stage- or size-dependent interactions in IGP systems model life-history omnivory as an ‘ontogenetic niche widening’ instead of an ontogenetic niche shift (van de Wolfshaar et al. 2006, Rudolf 2007). Such a niche widening implies that additional resources become available when intraguild predators grow in size. In this case, juvenile predators only feed on resources, while adult predators are involved in IGP and hence prey on both resource and consumers. Such a configuration still allows the intraguild predator to exclude the consumer, since adult predators can exclusively forage on resource biomass when productivity levels are high (van de Wolfshaar et al. 2006).

IGP is not only a common phenomenon, but more omnivorous species also coexist in the same habitat (Polis 1991, Polis and Strong 1996, Arim and Marquet 2004). Coexistence of multiple intraguild predators has been studied to a limited extend (but see HilleRisLambers and Dieckmann 2003) compared to the vast literature existing on the effects of single intraguild predators on the persistence of a community. Persistence of multiple intraguild predators without life-history omnivory in a community has been deemed even more difficult than persistence of a single intraguild species in the community. HilleRisLambers and Dieckmann (2003) showed, using unstructured populations of two intraguild species preying on each other and feeding on a single common resource, that coexistence of intraguild predators is limited to a small parameter region.

In this paper, we study the possibilities for coexistence of two intraguild predators, each structured into two life stages, where individuals undergo a niche widening as soon as they mature. We also relate the study on ontogenetic niche widening by van de Wolfshaar et al. (2006) with the study on ontogenetic niche shifts or life-history omnivory by Hin et al. (2011).

We set the diet of one population so that it feeds on resource and competitor half of the time (=niche widener) and vary the diet preference of adults in the other population. At one extreme the population only feeds on resource throughout its entire life, creating a community in which the predator is the niche widener. At the other extreme the adults exclusively prey on juveniles of the competitor and its juveniles feed on the resource (=life history omnivore), creating a community with a niche widener and a life history omnivore. We show that coexistence of intraguild predators is stable if either of these extremes is approached.

The model predicts extended coexistence possibilities when the community consists of both a niche widener and a life history omnivore. In this case a balance between competition and predation can lead to equilibrium coexistence over a large range of productivities, but this equilibrium is generically unstable. Stable coexistence only occurs when community dynamics are shaped primarily by predation with competitive interactions playing only a marginal role. As a result, community dynamics in stable coexistence largely resemble those of a three-species linear food chain. In contrast, community dynamics may also be governed by strong competition between niche wideners and life history omnivores, leading to an alternative stable state, in which juvenile niche wideners outcompete juvenile life history omnivores by imposing a juvenile bottleneck.

2 Materials and Methods

The ontogenetic changes in feeding habits of intraguild predators are modeled using the bioenergetics approach of Yodzis and Innes (1992) with a stage-structured extension as formulated by De Roos et al. (2007b). Five ordinary differential equations (ODEs) keep track of biomass changes of resource *R*, and two intraguild predators *P* and *G* (juveniles P_j and G_j and adults P_a and G_a , see table 1 below).

Table 1: Ordinary differential equations

$$\frac{dR}{dt} = \delta(R_{\max} - R) - M_p \frac{R}{H_p + R} P_j - M_p \frac{0.5R}{H_p + 0.5R + 0.5G_j} P_a$$

$$- M_g \frac{R}{H_g + R} G_j - M_g \frac{\Phi R}{H_g + \Phi R + (1-\Phi) P_j} G_a$$

$$\frac{dG_j}{dt} = v_{ga}(R, P_j) G_a + v_{gj}(R) G_j - \gamma_g(v_{gj}(R)) G_j - \mu_{gj}(P_a) G_j$$

$$\frac{dG_a}{dt} = \gamma_g(v_{gj}(R)) G_j - \mu_b G_a$$

$$\frac{dP_j}{dt} = v_{pa}(R, G_j) P_a + v_{pj}(R) P_j - \gamma_p(v_{pj}(R)) P_j - \mu_{pj}(G_a) P_j$$

$$\frac{dP_a}{dt} = \gamma_p(v_{pj}(R)) P_j - \mu_b P_a$$

Resource follows semi-chemostat dynamics in absence of *P* and *G*, with turnover rate *δ* and maximum resource density R_{max}. Resource decreases through feeding by *P* and *G*.
Both intraguild predators are structured into a juvenile and an adult stage and feed on both juveniles of the other predator and resource biomass.

Adult biomass decreases through background mortality μ_b *only*, while juvenile biomass decreases through predation by predators and background mortality, combined in the terms $\mu_{pj}(G_a)$ and $\mu_{gj}(P_a)$ for P_j and G_j respectively (see below for details). Juvenile net biomass production, v_{ij}, is used for growth of juveniles and maturation, which is represented by the mass-specific rate γ_i. Net biomass production of adults, v_{ia}, is only used for production of juveniles so intraguild predators do not grow any further after entering the adult stage. The mass-specific maturation rate is derived from (De Roos et al. 2007b) and given by:

$$\gamma_i = \frac{v_{ij} - \mu_i}{1 - z^{1-\mu_i/v_{ij}}} \qquad (1)$$

Maturation depends on net biomass production of juveniles, v_{ij}, predator background mortality μ_b and the ratio of predator body size at birth and at maturation, represented by the parameter *z* (De Roos et al. 2007b). Equation (1) captures the growth and survival of juvenile individuals from the size at birth to the size at maturation in such a way that the stage-structured biomass model in equilibrium is exactly identical to a physiologically structured population model (PSPM) accounting for a continuous size-distribution of juvenile predators (De Roos et al. 2008b).

Mass-specific net biomass production of juveniles and adults, denoted by v_{ij} and v_{ia}, respectively, equal the difference between mass-specific ingestion and mass-specific maintenance T_i. Ingestion follows a type II functional response with maximum ingestion M_i, half-saturation constant H_i and conversion efficiency σ. Parameter Φ models the extent of ontogenetic diet shift between juveniles and adults of predator G. Although Φ represents differences in feeding habits rather phenomenologically, it can be interpreted as the relative time spent by adults feeding on a particular prey species. At Φ = 1, no diet shift occurs and both stages of G feed on the resource R. When Φ <1, however, individuals broaden their diet after adulthood and start feeding on juvenile competitors (P_j). At Φ = 0.5, adults spend half their time feeding resource and half on juvenile competitors. At Φ = 0, the intraguild predator G experiences a full diet shift over ontogeny; it is a life-history omnivore: juveniles feed on the resource only and adults feed on juvenile competitors only. We assume adults of the other intraguild predator, P_a, always feed on both resource and juvenile competitors (G_j) equally. Hence mass-specific net biomass production rates for both juvenile predator stages P_j and G_j are given by

$$v_{ij}(R) = \sigma M_i \frac{R}{H_i + R} - T_i$$

The mass-specific net biomass production rates for adults G_a and P_a are given by

$$v_{ga}(R, P_j) = \sigma M_g \frac{\Phi R + (1-\Phi) P_j}{H_g + \Phi R + (1-\Phi) P_j} - T_g$$

$$v_{pa}(R, G_j) = \sigma M_p \frac{0.5 R + 0.5 G_j}{H_p + 0.5 R + 0.5 G_j} - T_p$$

The predatory interaction between the two predators lead to mortality rates for each juvenile stage according to:

$$\mu_{pj}(G_a) = \mu_b + \frac{(1-\Phi) G_a M_p}{H_p + \Phi R + (1-\Phi) P_j}$$

$$\mu_{gj}(P_a) = \mu_b + \frac{0.5 P_a M_p}{H_p + 0.5 R + 0.5 G_j}$$

We will vary Φ to show the effects of these diet changes in one predator on the community.

2.1 Model Parameterization

The model is parameterized to describe the dynamics between sprat and herring using similar rates as in van Leeuwen et al. (2008). Furthermore, we assume that all parameters, except Φ are the same in both populations. This way we can isolate the effects of changing Φ on community dynamics from effects of other differences between populations. The stage-structured biomass model and its parameterization as used here, is such that the results presented in this report are more generally applicable to interactions between all sorts of organisms (De Roos et al. 2007a, De Roos et al. 2008a, Schellekens et al. 2010). Default model parameters are summarized in table 2.

Table 2: Default model parameters

Parameter	Resource	Predator *G* and *P*	Description
R_{max}	varied		Resource maximum biomass density
δ	0.1		Resource turn-over rate
σ		0.5	Assimilation efficiency
M		0.23	Maximum ingestion rate (mass specific)
T		0.032	Maintenance rate (mass specific)
μ_b		0.001	Background mortality rate
H		1	Half-saturation constant
Φ		varied in *G*	Adult time spend feeding on either *P* or *R*
z		0.035	Newborn-adult predator size ratio

Maximum ingestion (M) and maintenance (T) are both mass-specific rates (expressed in unit biomass per unit biomass per unit time), whereas the mortality parameter (μ) represents a per-capita rate.
The maximum resource density R_{max} and half-saturation density H are expressed as gram biomass per unit volume and therefore the only parameters containing the unit of volume. H can be set to 1 without loss of generality, as this merely implies a scaling of the unit of the total system volume. Maximum resource density R_{max} is then expressed as multiples of the half-saturation density. A conversion efficiency of 0.5 is used for conversion of both resource and consumer biomass (Peters 1983).
Model predictions are analyzed for different values of R_{max} and Φ. Maximum resource densities R_{max} correspond to different productivity levels which equal δR_{max}. We will hence use maximum resource density and resource productivity as synonyms. We used Content, a numerical bifurcation software package (Kuznetsov et al. 1996), to calculate equilibrium densities as a function of R_{max} and Φ and to assess equilibrium stability.

3 Results

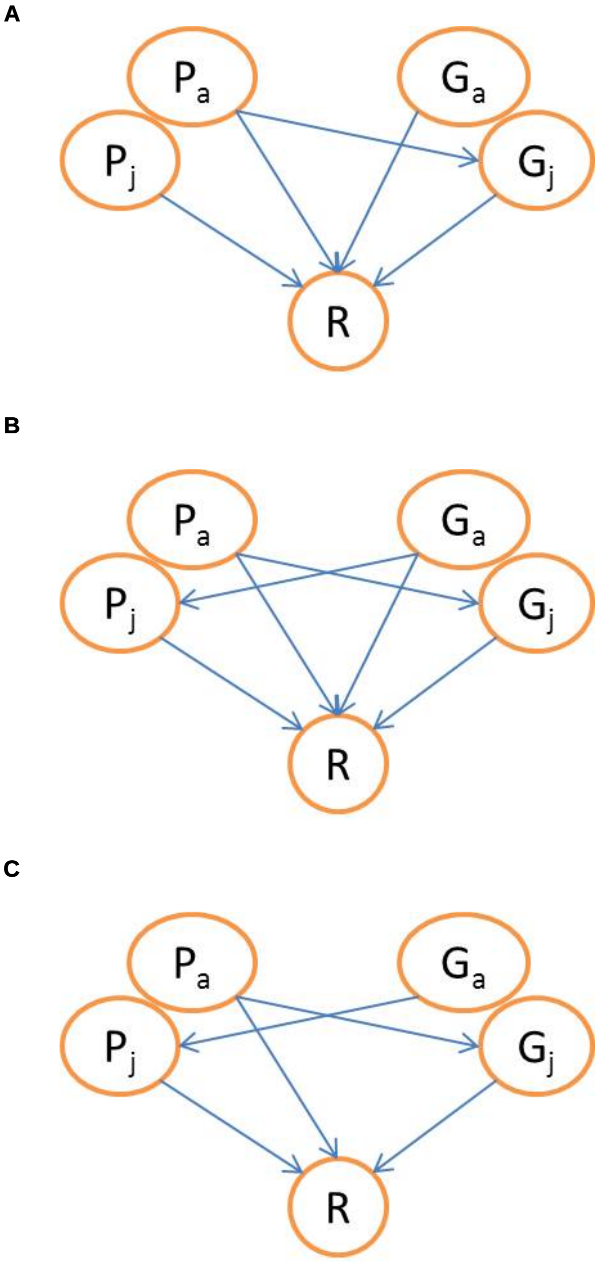

Figure 1: Three community configurations resulting from different settings of Φ*, the parameter that distributes the time of* G_a *spend feeding on* P_j *and R . A:* $\Phi=1$*, B:* $\Phi=0.5$*, C:* $\Phi=0.0$*.*

We start out by assuming $\Phi=1$ (Figure 1A).
This configuration lets population *G* feed on resource *R* throughout its life. Therefore, the interaction between *G* and *P* is one that is similar to a classic intraguild predation scheme, like the one presented by Mylius et al (2001), where the intraguild predator (*P*) is a poorer resource competitor than population *G* (=consumer), but feeds on G_j. However, like in van de Wolfshaar et al. (2006) the adults of predator *P* have widened their niche compared to juveniles, feeding on both resource and juvenile competitors (G_j). Just like in the unstructured IGP system (Mylius et al. 2001) in our system at $\Phi=1$ four equilibrium types occur: 1) a resource-only equilibrium; 2) a consumer-resource equilibrium; 3) a coexistence equilibrium with resource, consumers and intraguild predators and 4) a predator-resource equilibrium (figure 3, right

panel). The resource-only equilibrium is stable when growth rates of consumers and predators are negative. Since consumers have lower resource requirements than predators (i.e. $R_g^* < R_p^*$) consumers invade the resource-only equilibrium when predator growth rate is still negative. In the consumer-resource equilibrium, resource density stays constant at R_g^* while consumer density G increases with increasing R_{max}, thus increasing adult predator (P_a) food availability. Invasion of predators (P) in the consumer-resource equilibrium becomes possible when net biomass production of predators becomes high enough to overcome their background mortality and the life time reproduction equals 1. The life time reproduction of this stage-structured biomass model population has been formulated by (De Roos 2008) and is expressed as:

$$\frac{\nu_{pa}}{\mu_b} z^{\frac{\mu_{pj}}{\nu_{pj}}-1} = 1 \qquad 1$$

This productivity threshold is denoted as the invasion point of population P (I_p; figure 3, right panel). Increasing productivity in the coexistence equilibrium increases predator P and resource biomass and decreases consumer G biomass. At a particular resource productivity a stable predator P-resource equilibrium becomes possible. This productivity level is denoted as the consumer invasion point, since it is the highest R_{max} value, for which consumers (G) can invade the predator-resource equilibrium (not shown here). Increasing productivity in the coexistence state eventually leads to exclusion of consumers, as predation pressure becomes too high for their persistence. This threshold is referred to as the consumer exclusion point (E_g). These two threshold levels of productivity may not coincide, as discussed in the study by Mylius et al. (2001), resulting in bistability with the coexistence equilibrium and the predator-resource equilibrium as alternative stable states. Here, consumers can persist when present, but are unable to invade when absent due to high predation pressure. In the stage-structured model at these parameter settings the two thresholds do coincide. For simplicity we will refer to these coinciding thresholds as E_g. Beyond E_g, the predator-resource equilibrium is the only stable state.

Decreasing Φ decreases the use of resource by population G. Therefore, more resource productivity is needed in absence of predator P to match the resource requirements of G; the single population invasion threshold increases with Φ (visible in figures 2 and 4 as the solid gray line). Until $\Phi=0.5$, however, its resource requirements remain below that of P (figure 2). Decreasing Φ simultaneously enables the adults of population G to feed on P_j. Population P now endures higher mortality. Furthermore, because population G shifts its diet to feeding on P_j and therefore needs more resource to reach the same biomass, the invasion threshold of P (I_p, equation 1) is only satisfied at higher R_{max} when decreasing Φ. Because of the increasing predation on P_j, P needs ever more resource productivity to compensate for those losses, even though the competitive difference between G and P for resource becomes smaller with decreasing Φ. At a certain point the invasion point of P (I_p) crosses the exclusion point of population G (E_g), resulting in a single threshold I_p. This makes predator invasion and therefore coexistence unstable (figure 3, left panel dotted lines). As a consequence, from I_p onwards predators P eliminate G without the possibility for coexistence.

If $\Phi=0.5$, as in figure 1B, both predators have equal feeding and production rates and hence all invasion thresholds become one point (see figures 2 and 4).

Because all other parameters are assumed to be equal between G and P neutral coexistence occurs. We will not further discuss the results in this setting.

When $\Phi<0.5$ population G will be a more efficient predator but a poorer resource competitor than population P; the roles are reversed (figure 5, note the (trophic) position of P and G); when $\Phi<0.5$: $R_g^* > R_p^*$ and population P becomes the more efficient resource consumer. At low resource productivity population P will be able to exclude population G by resource competition. Increasing productivity at low enough Φ (below 0.34 in this case) will enable population G to invade, because it can prey on P_j and lower their effect on resource depletion, creating a balance between predation and resource competition. This results in a new productivity threshold: I_g, which, like equation 1, can be expressed as the life-time reproduction equal 1 for population G:

$$\frac{\nu_{ga}}{\mu_b} z^{\frac{\mu_{gj}}{\nu_{gj}}-1} = 1 \qquad (2)$$

Increasing productivity further and predator *G* can exclude *P*, but there is an alternative stable state. When *Φ* is nearly zero, adults of predator *G* require P_j to sustain, such that *P* can no longer be excluded.

As shown in figure 5, decreasing the value of *Φ* towards zero shifts the position of I_g toward higher R_{max} – values, while the productivity threshold from where coexistence is possible (E_g) changes less rapid over R_{max}. Ultimately this results in the equilibrium configuration as illustrated in figure 5 (right panel) for *Φ* = 0. In coexistence the community at *Φ* = 0 consists of two distinct types of intraguild predators: a life history omnivore (*G*) and an ontogenetic niche widener (*P*) (see figure 1C). G_a now solely prey on juvenile competitors (P_j), while G_j only forage on the resource just like P_j, and P_a feeds on both resource and juvenile competitors (G_j).

Due to the competitive advantage of *P* the single population invasion threshold of *G* disappeared and the *P* -resource equilibrium is stable for all R_{max} – values (visible at *Φ* = 0 in figure 5 as the solid gray line). Like Hin et al. (2011) describe for their system with one intraguild predator and prey, the introduction of predator *G* in our system is hampered by a juvenile bottleneck created by the competitive advantage of *P*. As an alternative outcome of dynamics a stable coexistence state exists. Since G_a lack an alternative resource at *Φ* = 0, *P* cannot be excluded from the coexistence state. Therefore, at low *Φ* – values the only productivity threshold present is E_g, marking the lower limit of R_{max} for which the intraguild predator *G* can persist in coexistence (figure 5, right panel). In this coexistence state equilibrium patterns with increasing productivity largely resemble those of a three-species linear food chain (Oksanen et al. 1981) where top predators (*G* in this case) regulate biomass of consumers (*P* in this case) and thus release the consumer's control over resource biomass. Density of *P* therefore stays constant with changing values of R_{max}, leading to bottom-up regulation of resource biomass in equilibrium, which increases with increasing R_{max}. Under these conditions, predation by adult predators G_a acts as the main structuring force and population *P* is top-down regulated by adult predators G_a, which nullifies the potentially strong competition between juvenile predators G_j and P_j. This cultivation by adult predators G_a increases food availability for juvenile predators G_j and enables their coexistence with population *P*. In the alternative, consumer (*P*)-resource equilibrium, strong competition for resources between juvenile predators G_j and P_j translates into a juvenile competitive bottleneck in population *G*, which restricts maturation and thereby marginalizes the predatory interactions between P_j and G_a. Under such conditions interspecific competition is the main structuring interaction in the community leading to predator *G* exclusion.

4 Conclusions

Intraguild predators can coexist. Although it was clear that they can from empirical observations (Polis 1991, Polis and Strong 1996, Arim and Marquet 2004), it was less clear from a theoretical point of view. Classical (unstructured) population dynamical theory has yielded two general mechanisms explaining how and why the coexistence of two intraguild predators would be unstable. Firstly, two consumers feeding on the same resources compete until the weaker competitor is excluded (Gause 1934). Secondly, an intraguild predator is able to exclude the consumer at high resource productivity by predation because it can sustain on resource alone (Mylius et al. 2001). Intraguild theory shows that coexistence between predator and prey is limited to intermediate resource productivity because only there a balance is possible between competition and predation, such that prey do not undergo too much mortality and predators not too much competition. When two unstructured intraguild predators are combined, coexistence requires both to set its trophic role (HilleRisLambers and Dieckmann 2003). One is a weak predator but a strong predator and the other is a weak predator but a strong competitor. This way a balance between intake and competition can be found again. This configuration narrows the possibilities for coexistence compared to the standard intraguild scheme with only one predator and its prey, but maintains the necessity for intermediate productivity levels for coexistence (HilleRisLambers and Dieckmann 2003). A main conclusion from HilleRisLambers and Dieckmann (2003) is that the potential for coexistence between intraguild predators is maximized when species cannot both be good at too many things.

Contemporary structured population dynamical theory, however, comes with possible insights in how differences between differently sized individuals of the same population can also affect interspecific interactions and community dynamics. Hin et al. (2011) have shown that such a diet shift can enhance stability of coexistence of intraguild predator and consumer and can explain why such intraguild systems in nature often react as if a three-species linear food chain (Oksanen et al. 1981) where top predators regulate biomass of consumers and thus release the consumer’s control over resource biomass. We show that when the diets of two intraguild predators, each feeding on the resource and the other intraguild predators juveniles, are different enough, they will be able to coexist.

The community effects of $\Phi=1$ and $\Phi=0$ seem similar over resource productivity, four equilibrium types occur: 1) a resource-only equilibrium; 2) a consumer-resource equilibrium; 3) a coexistence equilibrium with resource, consumers and intraguild predators and 4) a predator-resource equilibrium. However, the equilibria are different (compare right panels of figures 3 and 5). This is because the interactions between the predators are different at $\Phi=1$ and $\Phi=0$. At $\Phi=1$ G does not feed on P_j, while P always feeds on G_j even when $\Phi=0$ and G_a exclusively feeds on Pj. In effect, at $\Phi=1$ the interactions are like the classic intraguild predator (P) and consumer (G) interaction, while at $\Phi=0$ both G and P are intraguild predators, P feeding on both resource and juvenile G, while G feeds on juvenile P exclusively. This difference between the two predators makes G the more efficient predator, while P is the more efficient resource consumer. Because of the differences in interactions, the approach to invasion of the second predator and possibly coexistence at $\Phi=1$ and $\Phi=0$ are also different. Where at $\Phi=1$ an increase in resource productivity can enable a small biomass of the intraguild predator to invade the system, such an invasion is impossible at $\Phi=0$. At $\Phi=0$ the equilibrium with only the most efficient resource consumer present (P) is stable at all levels of resource productivity above the minimum resource requirements for P. Predator G is excluded by resource competition; juvenile predators Gj are not only preyed on by Pa but also experience a developmental bottleneck because resource is depleted and therefore cannot grow into adulthood. Invasion of the more efficient predator (G) is only possible if maturation of juveniles is possible. Maturation only takes place if resource is high enough, so successful invasion is possible if the predator can inflict enough mortality on its competitor (P) such that resource is raised above the minimum required for juvenile predators (Gj) to mature. These invasion requirements are similar to the one found by Hin et al. (2011). They considered a life-history omnivore (like predator G) and a consumer feeding only on resource. Even though we consider two intraguild predators, dynamically we get similar results as in a system with an intraguild predator with life-history omnivory and a consumer. The main conclusion of the analysis of Hin et al. (2011) is that because the life-history omnivore has split its roles over lifetime (a predator as adult and competitor as juvenile) the effect of these roles on community dynamics is split as well. Either the omnivore acts as a competitor (often the worse competitor and is excluded with increased resource productivity) or it acts as a predator. In the last case, community dynamics follow simple trophic interactions with three trophic levels. Our life history omnivore (*G*) does exactly the same. And even more, both predators put together, community dynamics force the two predators in their most efficient role: one is predator (*G*), one is consumer (*P*), irrespective of their potential roles.

In summary, coexistence of two life history omnivores is possible resulting in either intraguild dynamics (exclusion of prey at higher resource productivity) or tritrophic dynamics (increased productivity leads to increased predator biomass and keeps consumer biomass constant). Which of the two omnivores assumes the role of predator or prey depends on the efficiency of these roles compared to the other omnivore. If one omnivore is better in preying on juvenile competitors than its competitor is, it will assume the role of the predator.

Even though life history omnivores feed from multiple trophic levels and are both predator and consumer, they only affect community dynamics as a predator or consumer. The role-play of life history omnivores and its simple result on community dynamics can therewith explain the persistence of natural systems combined with the apparent ubiquity of omnivores in nature.

5 Figures

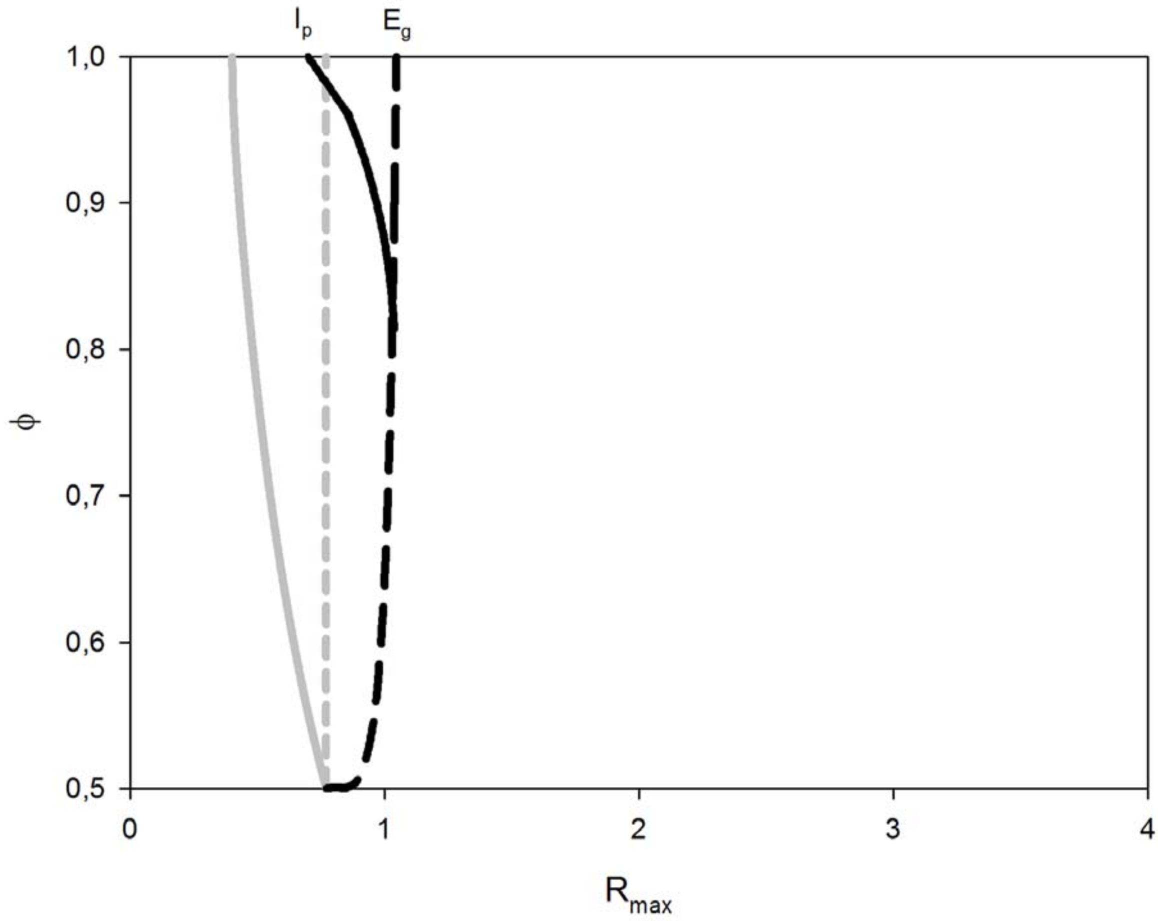

Figure 2: Φ over R_{max} *Changing positions of the productivity thresholds changing Φ from 1 to 0.5 (G is better competitor, but weaker predator than P). Gray lines: single population invasion thresholds (solid: invasion threshold of G, dashed: invasion threshold of P). Black lines: coexistence thresholds (dashed:* E_g*, solid:* I_p*).*

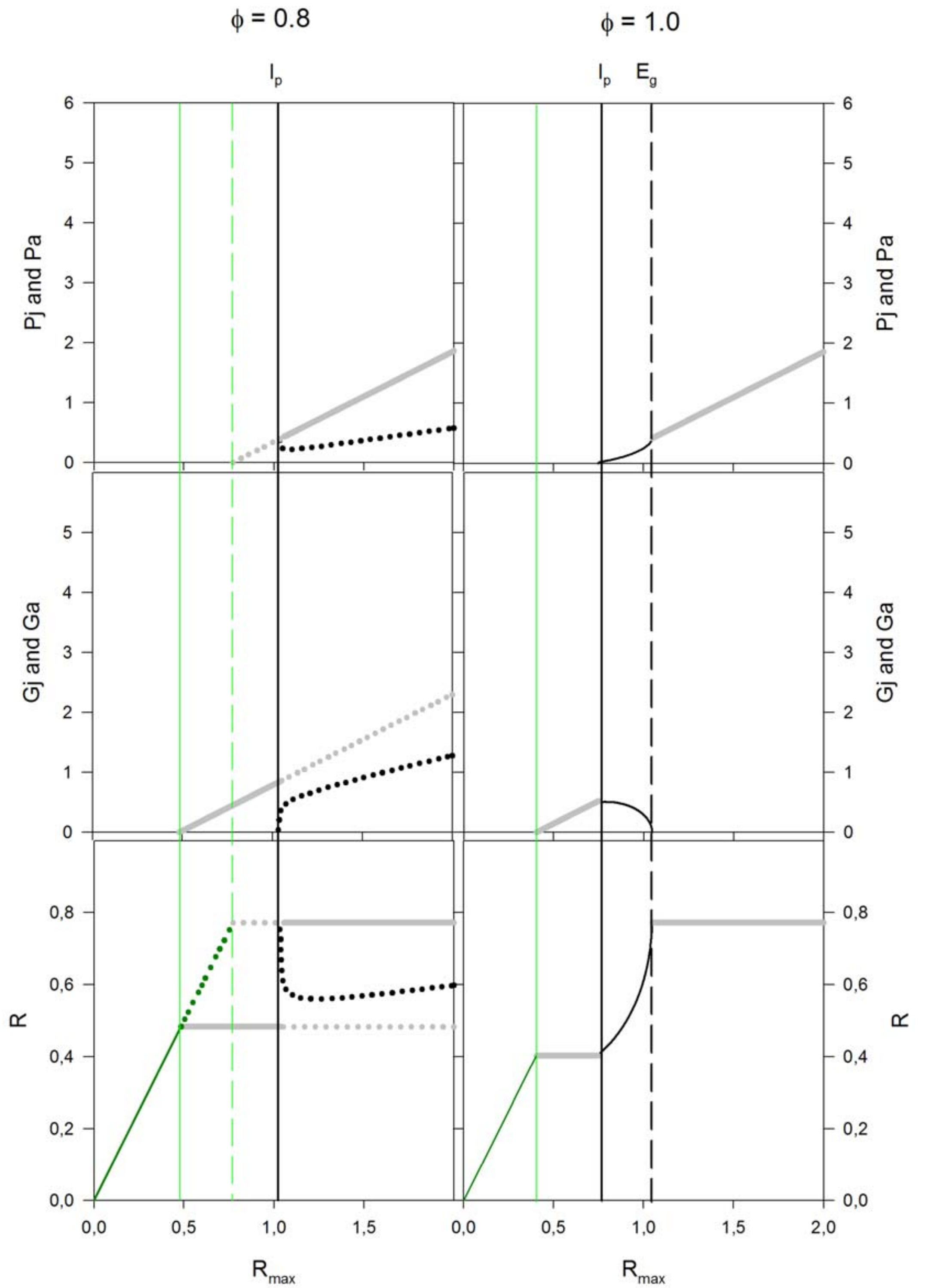

Figure 3: Biomass equilibria of P, G (both juveniles and adults combined) and R over R_{max} (from top to bottom panels reflecting trophic position) at two values of Φ: 0.8 at the left and 1 at the right panels (G is better competitor, but weaker predator than P). Dotted equilibria: unstable. Solid equilibria: stable (green: resource only equilibria, gray: single population equilibria, black: coexistence equilibria). Green vertical lines: single population invasion thresholds (solid: lowest threshold (G), dashed: highest threshold). Black vertical lines: coexistence thresholds (solid: I_p, dashed: E_g)

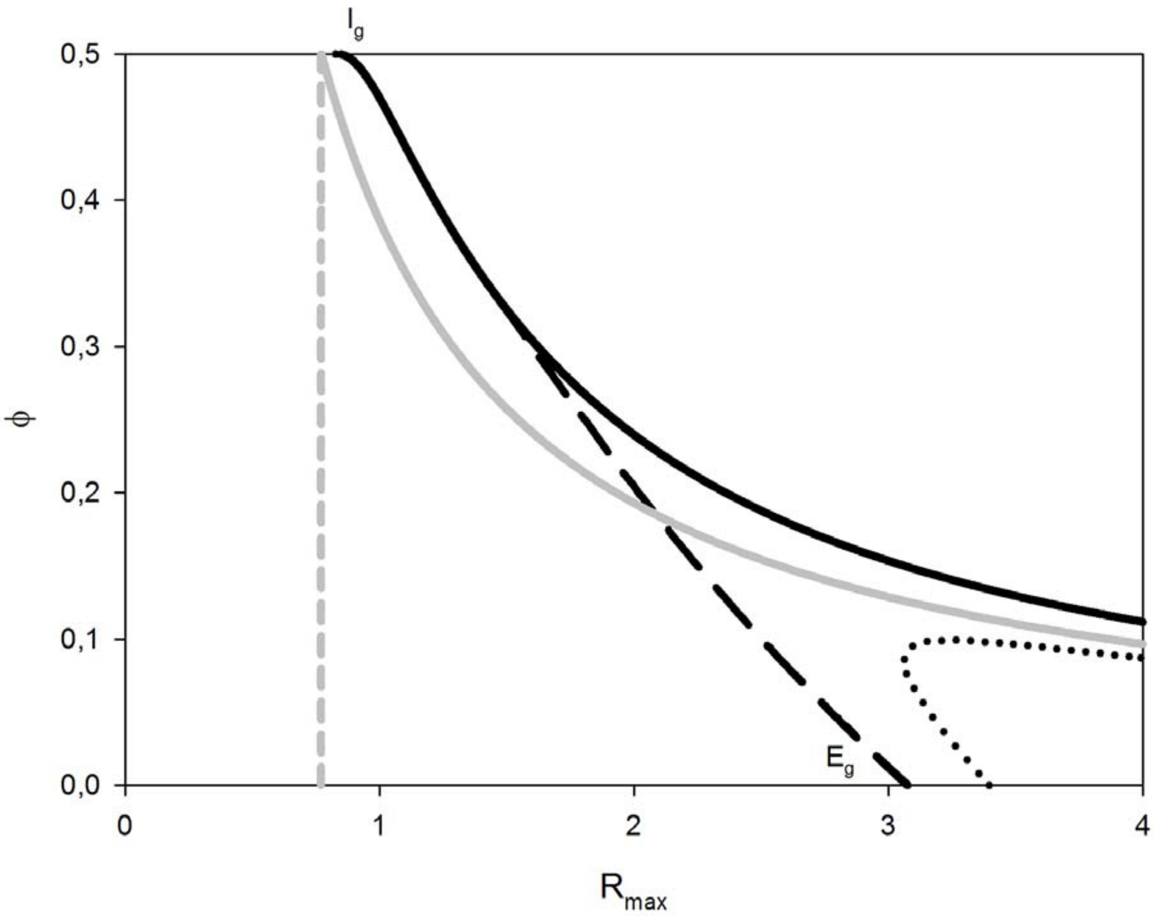

Figure 4: Φ over R_{max} Changing positions of the productivity thresholds changing Φ from 0.5 to 0.0 (G is worse competitor, but stronger predator than P). Gray lines: single population invasion thresholds (solid: invasion threshold of G, dashed: invasion threshold of P). Black lines: coexistence thresholds (solid: I_g, dashed: E_g, dotted: start of limit cycles)

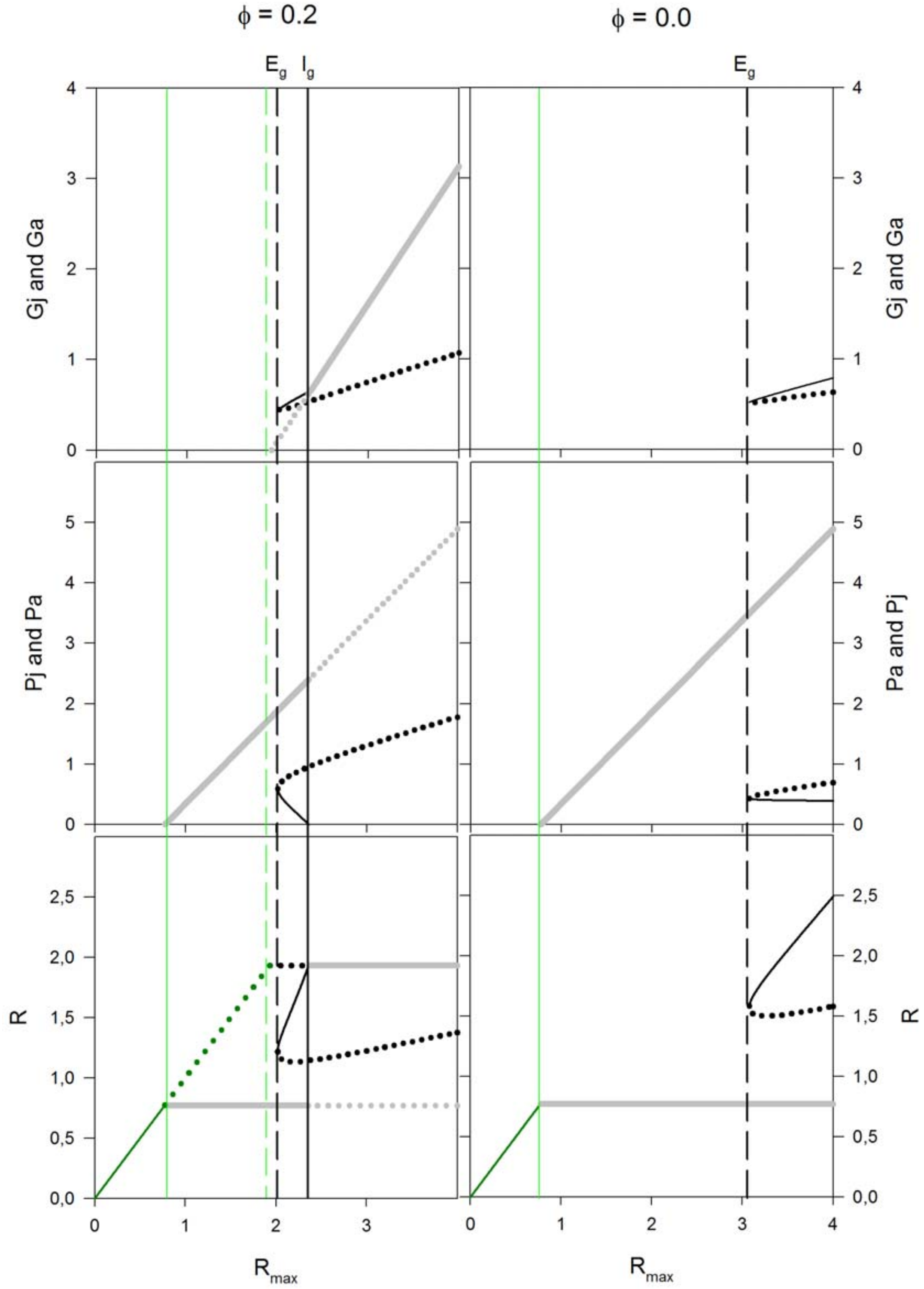

Figure 5: Biomass equilibria of G, P (both juveniles and adults combined) and R over R_{max} (from top to bottom panels reflecting trophic position) at two values of Φ: 0.2 at the left and 0.0 at the right panels (G is better competitor, but weaker predator than P). Dotted equilibria: unstable. Solid equilibria: stable (green: resource only equilibria, gray: single population equilibria, black: coexistence equilibria). Green vertical lines: single population invasion thresholds (solid: lowest threshold (P), dashed: highest threshold). Black vertical lines: coexistence thresholds (solid: I_g, dashed: E_g).

6 Quality Assurance

IMARES utilizes an ISO 9001:2008 certified quality management system (certificate number: 57846-2009-AQ-NLD-RvA). This certificate is valid until 15 December 2012. The organization has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Environmental Division has NEN-AND-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 27 March 2013 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation.

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Justification

Report	C158/11
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The scientific quality of this report has been peer reviewed by a colleague scientist and one head of the department at IMARES.

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Date:	1 December 2011